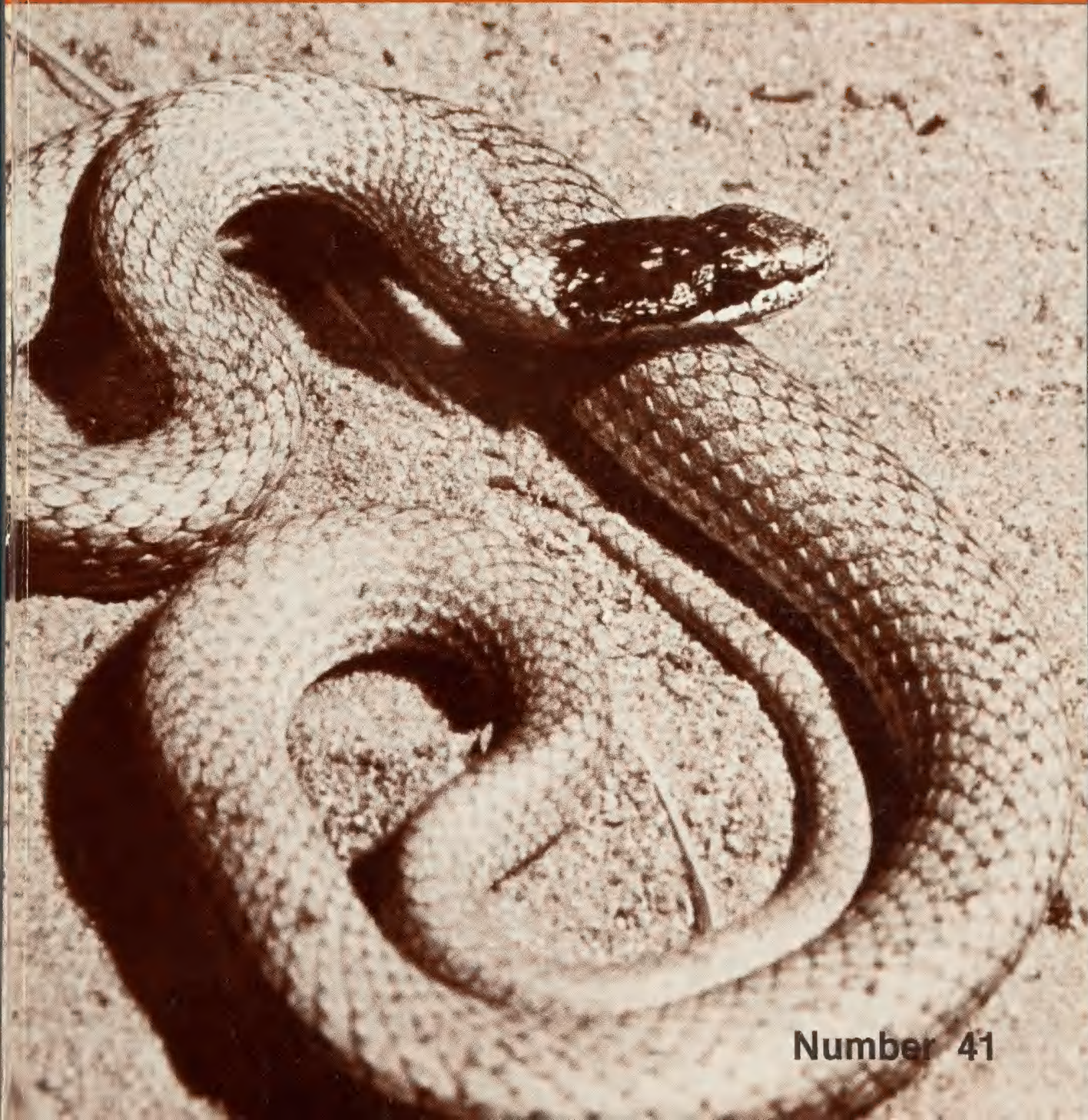


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TERTIARY SPECIES OF *ECHINOLAMPAS* (ECHINOIDEA) FROM SOUTHERN AUSTRALIA

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Abstract

Representatives of the genus *Echinolampas* are the most widely distributed cassiduloids occurring through the Tertiary rocks of southern Australia. Although some species were named by the turn of the century mostly they remain poorly defined and inadequately illustrated. In three nominal species the type material is lost and so there is need for the names to be stabilised. This paper presents a revision of all known species from southern Australia, including previously described species and three new forms: *E. posterocrassa curtata* subsp. nov., *E. gregoryi* sp. nov. and *E. gregoryi corrugata* subsp. nov. The ontogenetic development of *Echinolampas* is described and discussed.

Introduction

Echinolampas is a most compact, morphologically conservative and widely spread genus which achieved world-wide distribution throughout most of the Tertiary. According to Roman (1965, p. 689) more than 285 species have been recognised. Attempts to subdivide the genus have not found acceptance (Kier, 1962). The Indian Ocean species, *Echinolampas ovata* (Leske), which occurs along the north-west coast of Australia (Clark, 1946), represents the sole living representative occurring in Australian waters.

Material for this study came from collections in the British Museum (Natural History), London (BM); l'École des Mines, Paris; the National Museum of Victoria (NMV); the Western Australian Museum (WAM); Adelaide University, Geology Department (AUGD) and R. J. Foster.

Systematic Palaeontology

Order	CASSIDULOID	Claus, 1880
Suborder	CASSIDULINA	Claus, 1880
Family	ECHINOLAMPADIDAE	Gray, 1851
Genus	<i>Echinolampas</i>	Gray, 1825

Type species: Echinus oviformis Gmelin, 1789, by the subsequent designation of Pomel, 1883, p. 62.

Echinolampas posterocrassa posterocrassa
Gregory, 1890
(Pl. 1, Figs 1-6)

1890 *Echinolampas posterocrassus* Gregory, pp. 483-484, Pl. 13, figs 4.6.

- 1891 *Echinolampas posterocrassus* Gregory; Tate, p. 276
1892 *Progonolampas Novae-Hollandiae* Bittner, pp. 357-359, Pl. 3, fig. 1.
1892 *Echinolampas posterocrassus* Gregory; Tate, p. 193.
1892 *Echinolampas* cf. *posterocrassa* Gregory; Bittner, pp. 356-357.
1921 *Echinolampas (Miolampas) posterocrassa* Gregory; Lambert & Thiéry, p. 383.
1921 *Echinolampas (Progonolampas) Novae-Hollandiae* (Bittner); Lambert & Thiéry, p. 387.
1930 *Echinolampas posterocrassus* Gregory; Brighton, p. 569.
1930 *Echinolampas novae-hollandiae* (Bittner); Brighton, p. 569.
1946 *Echinolampas posterocrassa* Gregory; Clark, p. 359.
1948 *Progonolampas Novae-Hollandiae* Bittner; Mortensen, p. 272, figs 260a-c.
1962 *Echinolampas posterocrassus* Gregory; Kier, pp. 113-115, Pl. 32, figs 5-7, text fig. 66.
1965 *Echinolampas posterocrassa* Gregory; Roman, p. 295.

Type specimen: The holotype is the poorly preserved specimen figured by Gregory (1890, Pl. 13, figs 4-6) from 'Willunga, near Adelaide', and is registered in the British Museum (Natural History) as E3381.

Material, localities and horizons: Tate (1891, p. 276) recorded *E. posterocrassa* only from the 'glaucinitic limestone, Aldinga cliffs', i.e. the Tortachilla Limestone (early Late Eocene). The species has been collected from this formation in the Maslin Beach (north of Blanche Point) to Port Willunga district. In all, forty specimens from the Tortachilla Limestone have been studied. In addition twenty specimens have been recovered from an unnamed formation at Kingscote, Kangaroo Island, which is probably early Late Eocene in age, like the Tortachilla Limestone, and a further twenty specimens are known from the Nanarup Limestone member of the Late Eocene Werillup Formation near Nanarup, Western Australia.

Diagnosis: Test is low in small individuals, higher in larger individuals; sub-pentagonal in outline; apex set posterior of apical system, in small and medium-sized individuals, but almost coincident with it in largest individuals. Rostrum is well developed. Maximum width of test is posterior to apex. Apical system small and low, set one-third test length from anterior, bearing one to five tubercles. Ocular plates tumid adapically. Petals long and lanceolate, not closing distally. Pore-pairs circular and conjugate. Interporiferous zone narrow, poorly tuberculate, bearing, on average, one tubercle every other ambulacral plate. Poriferous tracts of petals markedly unequal in length. Adoral surface pulvinate with moderately depressed, sub-pentagonal peristome; bourrelets poorly developed. Sparsely tuberculate adorally; broad, non-tuberculate, sagittal tract present adorally on interambulacrum V.

Discussion: The collections from the Tortachilla Limestone reveal that only one species of *Echinolampas* is present. Tate (1892, p. 193) was of this opinion when he questioned the validity of Bittner's (1892) new genus and species *Progonolampas Novae-Hollandiae*. Bittner based his taxon on one of three specimens labelled *E. posterocrassa* sent him by Tate. Tate (1891, p. 276) held that *E. posterocrassa* was restricted to the 'glauconitic limestone, Aldinga cliffs', i.e., the Tortachilla Limestone, and (1892, p. 193) asserted that "the specimens forwarded to Vienna are authentic examples of Gregory's species", adding "I most strongly protest against such reckless species-making". Later workers (Kier, 1962, p. 115; Roman, 1965, p. 295) have followed Tate's interpretation. Bittner's (1892, Pl. 3, fig. 1) drawing of his specimen shows it to be very like *E. posterocrassa posterocrassa*, although somewhat unusual in its well-rounded posterior termination. Unfortunately Bittner's specimen is now lost. Although the available specimens of *E. posterocrassa posterocrassa* show little variation in outline, it is here concluded that Bittner based his new species on a specimen of *E. posterocrassa posterocrassa*. Reasons for regarding *Progonolampas* as a synonym of *Echinolampas* have been fully discussed by

Mortensen (1948, p. 278) and Kier (1962, p. 115).

In its well rounded shape and petals which are parallel-sided distally, *E. posterocrassa posterocrassa* compares with the younger *E. morgani*. It can be distinguished, however, by its larger size (up to 60mm test length), broader test, more medially positioned apex, smaller apical system with tumid ocular plates, longer poriferous tracts which are more unequal in length, and conjugate pore-pairs. In *E. morgani* (as in *E. gambierensis* and *E. tatei*) interambulacrum V is fully tuberculated adorally; in *E. posterocrassa posterocrassa* a broad sagittal band bare of tubercles is present (Pl. 1, fig.

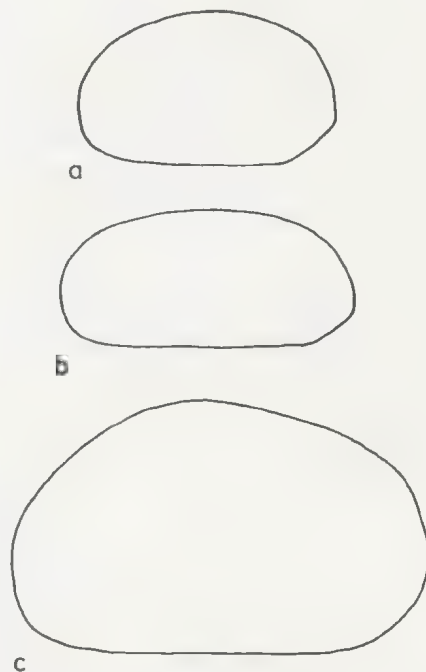


Figure 1—Lateral profiles of *Echinolampas posterocrassa posterocrassa* Gregory, 1890; a, NMV P55448, from the Tortachilla Limestone, Willunga, South Australia; b, WAM 72.52e from the Nanarup Limestone Member of the Werillup Formation of the Plantagenet Group, Nanarup Quarry, Western Australia; c, NMV P55446, from an un-named formation of Late Eocene age at Kingscote, Kangaroo Island, South Australia; all $\times 1$.

2); a similar zone exists in *E. ovula*, but it is much narrower.

The difference in lengths of the poriferous tracts of the petals is most marked in *E. posterocrassa posterocrassa*. In a specimen 35 mm in length the number of pore-pairs varies between 6 and 12. Even so, the difference is always greater than in *E. gambierensis*, *E. ovula*, *E. morgani* or *E. tatei*.

Specimens from the Late Eocene at Kingscote, Kangaroo Island referable to *E. posterocrassa posterocrassa* differ from topotype material only in the larger size attained. Some specimens from the Nanarup Limestone near Albany, W.A. tend to be slightly flatter than topotype specimens of corresponding test length (Fig. 1b). In all other respects they are identical with *E. posterocrassa posterocrassa* and so identified with the Tortachilla Limestone species. A collection from the younger Oligocene Port Vincent Limestone, however, shows sufficient differences to be distinguished as a separate subspecies of *E. posterocrassa*.

***Echinolampas posterocrassa curtata* subsp. nov.**
(P1. 1, figs 7-9)

Type specimen: The holotype of the subspecies is NMV P55451 from the Port Vincent Limestone in the Adelaide Cement Holdings Quarry, 4 km north of Wool Bay, east coast of Yorke Peninsula, South Australia (see McGowran *et al.*, 1971). Paratypes from the same locality are NMV P55452 and P55453.

Material, locality and horizon: In addition to the type specimens four other specimens are known from the same locality. This horizon is referred to the *Guembelitria stavensis* Zone (Stuart, 1970, p. 174) of the Oligocene and Zone P. 21 of Blow (1970).

Diagnosis: A subspecies of *E. posterocrassa* with short petals and swollen bourrelets; peristome and periproct small.

Discussion: The poriferous tracts of ambulacra I and V are shorter than those of *E. posterocrassa posterocrassa*, possessing on

average, three-quarters of the number of pores. Although *E. posterocrassa curtata* possesses relatively fewer pore-pairs than *E. posterocrassa posterocrassa*, the difference in length of the poriferous tracts in each petal is similar. The phyllodes of *E. posterocrassa curtata* are more sunken than those of *E. posterocrassa posterocrassa* and so the bourrelets are correspondingly more swollen. With growth of the test, swelling of the bourrelets was largely in a vertical direction so that the outline of the peristome remains oval. In *E. posterocrassa posterocrassa*, however, the swelling of the bourrelets (which occurred at a much later stage of growth than in *E. posterocrassa curtata*) was largely in a horizontal direction so that the peristome developed a pentagonal outline.

The slightly smaller periproct and peristome of *E. posterocrassa curtata* is apparent in comparing P1. 1, fig. 4, and P1. 1, fig. 8.

The trivial name for the new subspecies derives from the Latin *curtatus*, meaning "shorten".

***Echinolampas morgani* Cotteau, 1889**
(P1. 1, figs 10-13, P1. 2, figs 1-3)

- 1889 *Echinolampas morgani* Cotteau; pp. 546-547, P1. 12, figs. 13-15.
- 1891 *Echinolampas morgani* Cotteau; Cotteau, pp. 144-146, P1. 18, figs. 13-15.
- 1892 *Echinolampas gambierensis* Tenison Woods: Tate, p. 193 (*pars.*).
- 1921 *Echinolampas (Isolampas) morgani* Cotteau; Lambert & Thiéry, p. 380.
- 1930 *Echinolampas morgani* Cotteau; Brighton, p. 568.
- 1965 *Echinolampas morgani* Cotteau; Roman, p. 291.

Type specimen: The holotype, the single specimen on which Cotteau based this species, is an unnumbered specimen in the Cotteau Collection, École des Mines, Paris. It is from 'Mount Gambier', *i.e.*, the Gambier Limestone of Longfordian (Early Miocene) age.

Material, localities and horizons: Twenty-five specimens are known from the Gambier Limestone. In addition to those from Mt. Gambier, specimens have been collected from Peuker's Quarry, 5 km north-east of Mount Gambier, the Glenelg River north of Nelson in Victoria, and a quarry 2 km north of Nelson.

Additional material includes: twenty-two specimens from the Longfordian Mannum Formation from the cliffs of the Murray River between Swan Reach and Mannum; forty-one specimens from the early Early Miocene (probably Longfordian) Port Vincent Limestone from the sea cliffs between Giles Point and Coobowie; fourteen specimens from the same horizon in the Abrakurrie Limestone in the road cut where Highway 1 descends the Hampton Scarp at Madura, Western Australia.

Diagnosis: Test small and well-rounded; flat adapically with highest point almost two-thirds of the test length from the anterior end. Rostrum variably developed. Maximum width of test anterior to the apex. Apical system less than one-third test length from the anterior to the apex. Apical system less than one-third test length from the anterior end, well domed, and non-tuberculate. Petals short and lanceolate; not converging distally. Interporiferous zone narrow, flat and sparsely tuberculated, approximately one tubercle every ambulacral plate. Pores circular and not conjugate. Poriferous tracts within each petal differing only slightly in length. Adoral surface pulvinate with a quite deeply sunken, oval peristome. Floscelle small with bourrelets hardly developed; phyllodes small. Periproct at high angle (between 40°-55°) to the adoral surface.

Discussion: The only appreciable difference between specimens of *E. morgani* from the Gambier Limestone and those from the Mannum Formation is in the degree of development of the rostrum on the aboral interambulacrum V. It is always present in the Gambier Limestone forms (Pl. 2, fig. 2), but the material from both the Mannum Formation and the Port Vincent Limestone shows much more variation in this feature (Fig. 2). In some specimens, therefore, the rostrum is hardly developed, so that their outline is more circular (Pl. 1, fig. 13).

This species is characterised particularly by its low profile but tumid shape, and its short, lanceolate petals. Compared with other species of *Echinolampas* from the Australian Tertiary, *E. morgani* possesses the shortest petals with

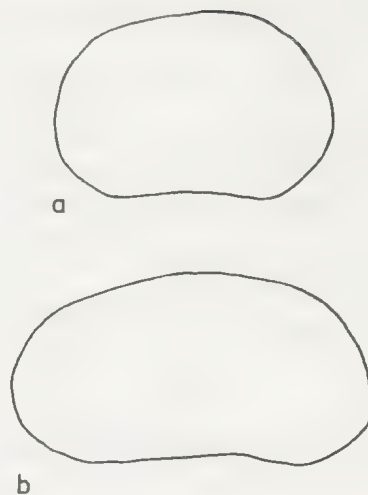


Figure 2—Lateral profiles of *Echinolampas morgani* Cotteau, 1889; a, NMV P55454, from the Mannum Formation, Murray River Cliffs, South Australia; b, NMV P19176, from the Gambier Limestone, Mt. Gambier, South Australia; both $\times 1$.

the fewest pore-pairs. The number of pore-pairs present in the longer poriferous tract in ambulacra I or V is somewhat variable, between 22 and 28 in a specimen of *E. morgani* 40 mm in length. By comparison, in specimens of similar size, *E. ovulum* has between 26 and 34, *E. gambierensis* between 32 and 35, and *E. posterocrassa* between 32 and 41 pore pairs (Fig. 5b).

Although *E. morgani* and *E. posterocrassa* have tests of similar size, they differ conspicuously in the apical system which in *E. morgani* is proportionately larger. In addition, whereas the ocular plates in *E. morgani* are depressed (as they are in *E. gambierensis*) they are domed in *E. posterocrassa*.

E. morgani is the smallest species of *Echinolampas* so far known from the Australian Tertiary. The largest test has a maximum length of 50 mm.

***Echinolampas ovulum* Laube, 1869 (Pl. 2, figs 4-8)**

- 1869 *Echinolampas ovulum* Laube, pp. 191-192.
- 1877 *Echinolampas ovulum* Laube; Duncan, pp. 44, 66.
- 1885 *Echinolampas ovulum* Laube; Tate, p. 37.
- 1885 *Echinolampas gambierensis* Tenison Woods; Tate, p. 41 (pars.).

- 1887 *Echinolampas ovulum* Laube; Duncan, p. 420.
 1890 *Echinolampas ovulum* Laube; Gregory, p. 483, ?P1. 13, figs 7-8.
 1891 *Echinolampas gambierensis* Tenison Woods; Tate, p. 276 (pars.).
 1892 *Echinolampas ovulum* Laube; Bittner, p. 357.
 1921 *Echinolampas* (*Miolampas*) *ovulum* Laube; Lambert & Thiéry, p. 383.
 1930 *Echinolampas ovulum* Laube; Brighton, p. 568.
 1965 *Echinolampas gambierensis* Tenison Woods; Roman, p. 281 (pars.).
 non 1847 *Echinolampas ovulum* Tallivignes; p. 1141 (*nomen nudum*).

Type specimen: The original specimen on which Laube founded this species is no longer in the collections of the Naturhistorisches Museum, Vienna, and must be presumed lost. It is not known for certain whether or not the specimen which Gregory (1890, P1. 13, figs 7, 8) attributed to *E. ovulum* does in fact belong to this species (see below). Consequently for taxonomic stability NMV P55457 (P1. 2, figs 4-7) from the Mannum Formation (Early Miocene) at Blanchetown, Murray River, is here chosen as neotype.

Material, localities and horizon: This species is represented in the collections by nine specimens, all from the Mannum Formation from the Murray River at: Swan Reach, Blanchetown, Nildottie, River Marne and Younghusband. It is not known from any other horizon or locality.

Diagnosis: Test large and of variable height (see P1. 2, fig 6 and Fig 3b), but is flattened adapically; rostrum moderately developed. Apical system close to mid-length. Petals very wide and confluent distally. Interporiferous zone flat to gently domed; poriferous tracts only slightly unequal in length. Pores well separated, inner smaller and more circular than tear-shaped outer pores; connected by long, narrow canal whose length equals twice the pore diameter. Each ambulacral plate bears 4-5 tubercles. Adoral surface moderately pulvinate. Periproct shallow and pentagonal. Floscelle with weakly tumid bourrelets and narrow phyllodes. Test densely tuberculate; tubercles large. A narrow sagittal band on the adoral surface of interambulacrum V lacks tubercles, but bears fine granules; these commonly occur between the tubercles on the adoral surface.

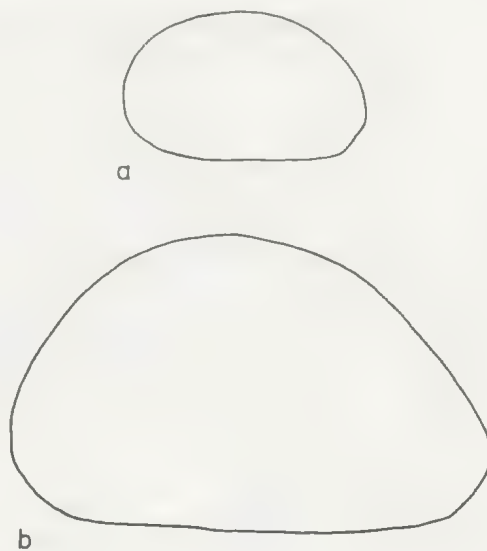


Figure 3—Lateral profiles of *Echinolampas ovulum* Laube, 1869; a, NMV P55459, from the Mannum Formation, River Marne, South Australia; b, NMV P55458, from the Mannum Formation, Nildottie, South Australia; both $\times 1$.

Discussion: This species has had a rather chequered history. Laube's (1869, p. 191) original description was brief and not accompanied by any illustration of the species. Although Duncan (1877, p. 66; 1887, p. 420) was convinced of the validity of the species, Tate (1885, p. 41) considered it synonymous with *E. gambierensis*. Duncan (1887, p. 420) gave some dimensions of a specimen which he considered to be *E. ovulum*, but provided no details concerning the locality from which it had come. Later, however, Gregory (1890, p. 483) published dimensions of Laube's specimen from the Murray cliffs, along with those of a specimen which he presumed to be that seen by Duncan (BM E1107); this specimen he figured (Gregory 1890, P1. 13, figs 7, 8). The specimen however is not from the Murray cliffs, but from 'Bairnsdale, Victoria'. Consequently it seems probably that this specimen is younger than the early Early Miocene (Longfordian) specimen of Laube. It is 57 mm in length (Gregory, 1890, p. 483), and has ambulacrum II 8 mm in width, and ambulacrum I 9.5 mm in width (Duncan, 1887, p. 420); there is little difference between the

lengths of the poriferous tracts (see Gregory, 1890, Pl. 13, fig. 8). A topotype of specimen *E. ovulum* (NMV P55460) of comparable length to the Bairnsdale specimen, has ambulacrum 1 8.6 mm in width. Gregory's (1890, Pl. 13, fig. 8) illustration of the lateral view of the Bairnsdale specimen shows a more conical form than seen in topotype material, and has the apical system set posterior of the mid-test length. As the Bairnsdale specimen cannot at present be located at the British Museum (Natural History) (D. N. Lewis, *pers. comm.* 3/5/78) it is considered advisable to identify it as *E. aff. ovulum*.

E. gambierensis, within which some workers (Tate, 1885, 1891; Roman, 1965) have placed *E. ovulum*, is, indeed, rather similar in the possession of a large (up to 67.8 mm in length), high test and broad, distally narrowing petals. *E. ovulum* can be distinguished, however, by its broader (Fig. 5a), flatter ambulacral interporiferous zone (Pl. 2, fig. 7), more separated pores, flattened aboral surface, more densely tuberculate test, more ovate dorsal outline (on account of the greater development of the rostrum), shallower periproct, less tumid bourrelets and narrower phyllodes. *Echinolampas ovulum* Tallivignes (1847) is merely given in a faunal list, and is apparently a *nomen nudum* which has never been validated.

***Echinolampas gambierensis* Tenison Woods,
1867
(Pl. 3, figs 1-7)**

- 1867 *Echinolampas gambierensis* Tenison Woods, p. 1, figs 1a-c.
- 1878 *Echinolampas gambierensis* Tenison Woods; Etheridge, p. 139.
- 1878 *Echinolampas australis* Tenison Woods; Etheridge, p. 139. (*lapsus calami pro E. gambierensis*)
- 1885 *Echinolampas gambierensis* Tenison Woods; Tate, pp. 37, 41 (*pars.*).
- 1891 *Echinolampas gambierensis* Tenison Woods; Tate, p. 276 (*pars.*).
- 1892 *Echinolampas gambierensis* Tenison Woods; Tate, p. 193 (*pars.*).
- 1921 *Echinolampas gambierensis* Tenison Woods; Lambert & Thiéry, p. 386.
- 1930 *Echinolampas gambierensis* Tenison Woods; Brighton, p. 568 (*pars.*).
- 1946 *Echinolampas gambierensis* Tenison Woods; Clark, p. 359 (*pars.*).
- 1965 *Echinolampas gambierensis* Tenison Woods; Roman, p. 281 (*pars.*).

Type specimen: The whereabouts of Tenison Woods' original specimen is not known, and it must be presumed lost. Consequently a neotype is selected (AUGD S35) from the Gambier Limestone of Longfordian (Early Miocene) age, from the quarry at the side of the road to Port Macdonnell, 6.5 km south of Mt. Gambier.

Material, localities and horizon: In addition to its occurrence in the Gambier Limestone in the region of Mt. Gambier, this species also occurs in the Gambier Limestone in the banks of the Glenelg River north of Nelson, Victoria. Sixteen specimens are known from the Gambier Limestone. In the penecontemporaneous Mannum Formation this species commonly occurs in the cliffs of the Murray River between Swan Reach and Mannum; twenty-eight specimens have been recovered.

Diagnosis: Test large and conical; apex slightly posterior of apical system. Apical system set more than one-third test length from anterior; tuberculate and gently domed. Petals broad, interporiferous zone five times width of poriferous tracts; raised and confluent distally. Poriferous tracts slightly unequal in length in each petal differing between four and seven pore pairs. Inner pores circular, outer tear-shaped; conjugate. Adoral surface is flattened. Periproct is shallow and pentagonal. Floscelle large, and has tumid bourrelets and broad phyllodes.

Discussion: Although, as in other species of *Echinolampas*, the height of the test varies intraspecifically, the conical form of the aboral surface, rising to a gently rounded apex at about mid-length in mature specimens (Fig. 4b) is characteristic of this species. *E. gregoryi* sp. nov. has a similar shaped aboral surface, but the apex and apical system are coincident, unlike *E. gambierensis* where the apical system is positioned anterior to the apex.

E. gambierensis differs from *E. morgani*, with which it occurs in both the Gambier Limestone and Mannum Formation, in a number of ways. In addition to its larger size (reaching a maximum known test length of 61

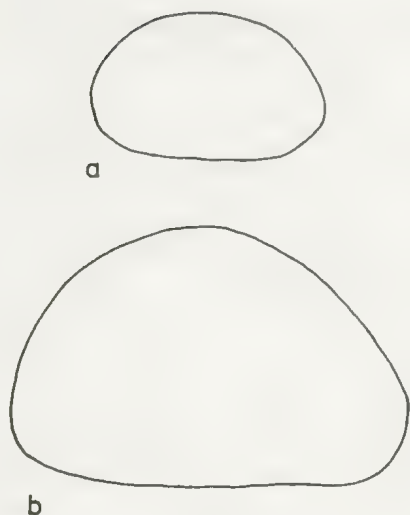


Figure 4—Lateral profiles of *Echinolampas gambierensis* Tenison Woods, 1867; a, from the Mannum Formation, Kroehn's Landing, Murray River, South Australia; b, AUGD S35, from the Gambier Limestone, Mt. Gambier, South Australia; both x1.

mm) and more conical test, *E. gambierensis* has longer and broader petals (Fig. 5a) which close distally and bear conjugate pore pairs; the outer pore is pear-shaped (P1. 3, fig. 4) whereas in *E. morgani* it is circular. The ambulacral plates of *E. gambierensis* are far more tuberculate than those of *E. morgani*, bearing 3-4 tubercles every plate, whereas those of *E. morgani* bear only one. *E. gambierensis* has a poorly developed rostrum, whereas it is well developed in specimens of *E. morgani* from the Gambier Limestone. The adoral surface of *E. gambierensis* is much flatter than in *E. morgani* with a larger floscelle with more tumid bourrelets.

Comparisons with the morphologically similar *E. ovulum* Laube are made under the discussion of that species.

Echinolampas tatei Lambert, 1898 (P1. 3, figs 8-11)

- 1893 *Conoclypeus rostratus* Tate, pp. 194-195, P1. 13, figs 1a-b. (non Mazetti, 1885).
1898 *Pleisiolampas rostratus* (Tate); Tate, p. 412.
1898 *Echinolampas tatei* Lambert, p. 165.
1921 *Echinolampas* (*Progonolampas*) *tatei* Lambert; Lambert & Thiéry, p. 387.

- 1943 *Conoclypeus rostratus* Tate; Crespin, p. 76.
1946 *Pleisiolampas rostrata* (Tate); Clark, p. 358.
1965 *Echinolampas tatei* Lambert; Roman, p. 302.

Type specimen: The holotype (P1. 3, figs 8-10) is AUGD T358, a specimen from 'Table Cape, Tasmania', figured by Tate 1893 (P1. 13, figs 1a-b), as *Conoclypeus rostratus* Tate. Preservation of the specimen is characteristic of the 'Upper Beds' (Fossil Bluff Sandstone) at Table Cape. These beds are Janjukian (Late Oligocene) in age (Gill, 1957).

Material, locality and horizon: In addition to the holotype, nine specimens are known from the 'Upper Beds' (Fossil Bluff Sandstone) at Table Cape. Preservation of material from Table Cape is poor, particularly that from the 'Upper Beds', from which all specimens are crushed to some extent. Material from the 'Lower Beds' (Freestone Cove Sandstone) has retained better the original shape. The species is not known from elsewhere.

Diagnosis: Test of moderate size, low, but conical. Rostrum well-developed; apex conjunct with, or slightly posterior of, apical system, which is set close to mid-length of test; gently domed. Petals broad and parallel-sided for most of their length; poriferous tracts of similar length. Pore pairs circular, conjugate (P1. 3, fig. 11). Adoral surface flattened, but with impressed ambulacra. Peristome oval and broad. Bourrelets barely developed. Tubercles large and closely spaced.

Discussion: Specimens of *Echinolampas* from Table Cape were originally described by Tate (1893) as '*Conoclypeus rostratus*'. Lambert (1898) considered that the species belonged, in fact, to *Echinolampas*. He also proposed a new name, *E. tatei*, as, in his opinion *Echinolampas rostrata* Cotteau 1894 from the Early Eocene of L'Oise had priority. In fact, Tate's *C. rostrata* predates Cotteau's name by one year. However, the name *E. rostrata* had been used earlier, by Mazetti (1885), although the species is considered (Roman, 1965, p. 297) to be synonymous with *E. angulata* Merian. Consequently, Lambert's name *E. tatei* is valid, but

Cotteau's *E. rostrata* is a homonym, requiring a new name.

E. tatei, which reaches a maximum test length of 54.1 mm, compares with *E. morgani* and *E. posterocrassa* in the possession of parallel-sided petals which show little distal closure. Like *E. morgani*, it has circular, though conjugate, pore pairs. These two species can further be distinguished by: the more pulvinate adoral surface of *E. morgani*; the broader ambulacral poriferous tracts, both adorally and aborally, in *E. tatei* (Fig. 5a); and the much higher inclination of the periproct in *E. morgani*.

The shape of the test of *E. tatei* bears some resemblance to small forms of *E. gambierensis* in which the test is low. The broader, distally narrowed petals of *E. gambierensis* and the greater rostral development in *E. tatei* serve to distinguish the two species.

In shape of the test, *E. tatei*, also compares with *Echinolampas westraliensis* (Crespin, 1943) from Cape Range, in north-west Western Australia, a species originally referred to *Conoclypus*. This Middle Miocene species, although having a similar test shape to *E. tatei*, has longer, wider and more petaloid ambulacra which possess slit-like outer pores.

***Echinolampas* aff. *tatei* Lambert, 1898**
(P1. 4, figs 1-3)

Material, locality and horizon: A single specimen (NMV P55466) from a marly lens within the Gambier Limestone, from the left bank of the Glenelg River at Nelson, Victoria.

Discussion: Of the two species of *Echinolampas* found in the Gambier Limestone this specimen most resembles *E. gambierensis*. However, it does not have the inflated aboral ambulacra, nor does it possess a well-developed floscelle, characteristic of *E. gambierensis*. The specimen more closely resembles *E. tatei* in its low, but conical test, low-angled periproct and flattened oral surface. *E. aff. tatei* can be distinguished from the Tasmanian species, however, by its possession of slightly longer poriferous ambulacral tracts, less well-developed floscelle and more centrally situated apical system.

***Echinolampas gregoryi gregoryi* sp. nov.**
(P1. 4, figs 4-6)

Type specimen: The holotype, and only known specimen, is NMV P18379, probably from the Bairnsdale Limestone (Middle Miocene).

Diagnosis: Test conical, apex and apical system coincident. Petals long, reaching almost to ambitus; broadening progressively abapically. Inequality in lengths of poriferous tracts in each petal small, about 4 pore pairs in ambulacrum I. Outer pores pear-shaped; weakly conjugate with smaller, rounded inner pores. Interambulacra raised above level of ambulacra. Within this raised area, a narrow, depressed zone extends along junction between interambulacral plates. Interambulacra also raised on oral surface. Peristome quite deeply sunken. Bourrelets weakly developed. Periproct inclined almost horizontally.

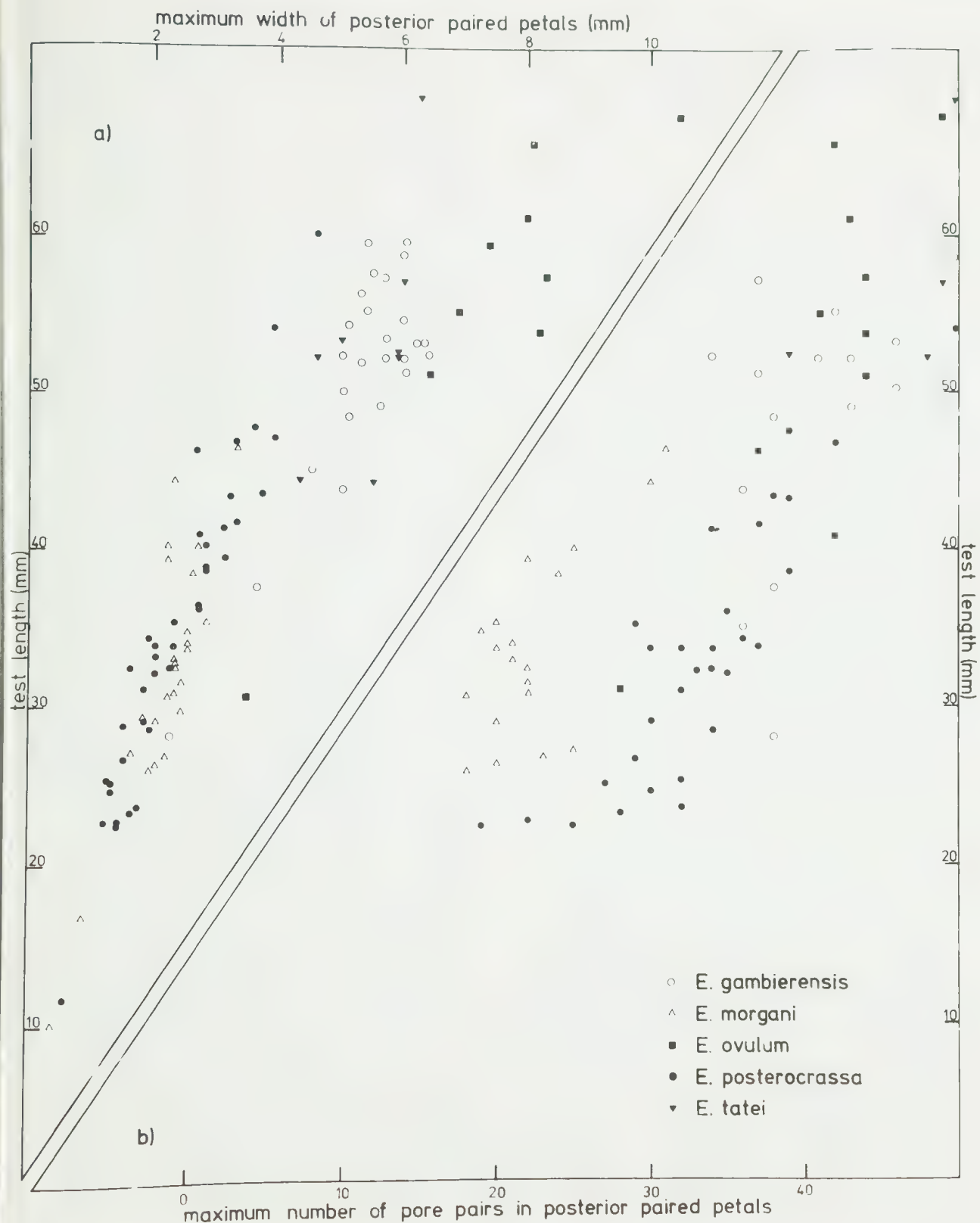
Discussion: *E. gregoryi gregoryi* shows a number of similar morphological features to *E. tatei*, in particular the test shape and form of the ambulacra. However, *E. gregoryi gregoryi* can be distinguished by its swollen interambulacra on both the adoral and aboral surfaces; ambulacral poriferous tracts of more equal length; and less well-developed bourrelets. *E. aff. tatei*, from the Gambier Limestone, is like *E. gregoryi gregoryi*, but lacks the swollen interambulacra and has a more oval peristome. *E. posterocrassa posterocrassa* has narrower, parallel sided petals, a flatter test, and a more pulvinate oral surface with a shallower peristome.

***Echinolampas gregoryi corrugata* subsp. nov.**
(P1. 4, figs 7-9)

Type specimen: The holotype and only known specimen is NMV P55477 from the Muddy Creek Formation at Clifton Bank, and is Balcombian in age (Middle Miocene).

Diagnosis: This subspecies differs from *E. gregoryi s.s.* by having: more swollen interam-

Figure 5— Plots of test length against, a: maximum width of posterior paired petals, and, b: maximum number of pore pairs in posterior paired petals for five species of *Echinolampas*.



bulacra, which do not possess the median depression; ambulacral poriferous tracts of very unequal lengths, in ambulacrum I difference being 12 pore pairs, in ambulacrum II, 15; oral surface flatter with shallower peristome.

Discussion: Of the two subspecies of *E. gregoryi*, *E. gregoryi corrugata* is the larger, being 68.7 mm in length, *E. gregoryi gregoryi* being 52.1 mm in length. The more highly vaulted test of *E. gregoryi corrugata* is considered to be a function both of the large size of the test (test height increasing at a greater rate than would be expected from normal allometric growth) and of slight dorso-ventral compression of the test of *E. gregoryi gregoryi*. The other large and often highly vaulted species of *Echinolampas* from the Tertiary of Australia is *E. gambierensis*. The two forms can be distinguished, however, by the raised petals of *E. gambierensis*; its distally narrowed petals; more swollen bourrelets; and higher angled periproct. The petals of *E. gregoryi corrugata* are relatively longer than those of *E. gambierensis*.

E. gregoryi corrugata compares with large specimens of *E. fraasi* de Loriol from the Middle Eocene of Somalia and Egypt (Kier 1957, p. 848, Pl. 103, fig. 12, Pl. 104, fig. 1) in shape of test and length and nature of the poriferous tracts. *E. fraasi*, however, has a more well developed floscelle and ambulacral poriferous tracts of more equal length.

Ontogeny of *Echinolampas*

In those Australian species of *Echinolampas* in which sufficient juvenile material is known (*E. posterocrassa*, *E. morgani* and *E. gambierensis*) the ontogenetic development is similar, but varies in the degree of morphological change. Although many features, such as form of the pore-pairs, degree of inequality of poriferous zones, position of the apical system and position of the peristome, remain constant through the growth series available, a number of other morphological features change. As the greatest ontogenetic changes occur in the oldest species, *E. posterocrassa*, most of the following discussion

is based on this species, although supplementary information is drawn from other species. Changes include:

(1) With increase in size of the test, the adapical surface changes from being low and flattened to being high and conical (Figs 1a,c,6). This trend has been noted previously by Kier (1957, p. 852) in *E. fraasi* de Loriol from Somalia. It is variable, for the change in height of the test is less in material of *E. posterocrassa* from the Nanarup Limestone, than in topotypes from the Tortachilla Limestone, perhaps suggesting that the feature may be controlled by environmental factors. *E. gambierensis* attains a conical test at an earlier growth stage than does *E. morgani* although there is some degree of intraspecific variation within each.

(2) With increase in size, the "apex" (the highest point of the test when the adoral surface is horizontal) moves forward (Figs 1a,c,3). Thus, in large individuals, the apical system may almost coincide with the "apex". This, in turn, results in a small change in the angle of orientation of the apical system to the plane of the adoral surface.

(3) There is a proportionate increase in length of the petals with growth of the test (Fig. 5b). Thus, in a specimen 22.5 mm in length, the petals of ambulacra I and V extend slightly less than half the length of the ambulacra (measured in a horizontal plane) to the ambitus (Pl. 1, fig. 5). In a specimen 38.5 mm in length, they extend four-fifths of the distance (Pl. 1, fig. 3) and in the largest known specimen of *E. posterocrassa* the petals almost reach the ambitus.

The rate of production of pore-pairs shows some important differences between species (Fig. 5b). A regular increase in the number of pore-pairs with growth is seen in *E. posterocrassa*. In *E. gambierensis*, however, the rate of development of pore-pairs is initially much greater so that almost the entire complement is attained when a length of about 30mm is reached, although the species may attain a length greater than 60mm. *E. morgani* is like *E. posterocrassa* for pore-pairs are produced reasonably constantly with growth (although at a reduced rate). The variations in rate of development of pore-pairs are illustrated in Fig.

5b and in the Table below which gives the number of pore-pairs for different sized specimens of the three species.

	small		large	
	length	pore-pairs	length	pore-pairs
<i>E. posterocrassa</i>	27mm	30	53mm	53
<i>E. gambierensis</i>	28mm	40	52mm	43
<i>E. morgani</i>	26mm	19	47mm	32

Within each petal, the difference in length of the tracts does not seem to change with growth (cf. Kier, 1957, p. 851), although such a difference appears more marked in small specimens because of the shortness of the petals. Intraspecific variation in equality of the length of the zones may be quite marked (see below).

(4) In *E. posterocrassa* the interporiferous zone is flat in small- and medium-sized individuals, being flush with the interambulacral surface. In specimens approximately 50mm in length, the interporiferous zone becomes slightly raised. This swelling increases with further growth of the individual, so that specimens 60mm in length have prominently swollen interporiferous zones, similar to those of medium-sized specimens of *E. gambierensis* and *E. ovulum*.

(5) The bourrelets become progressively more swollen with growth. In specimens over 40mm in length the bourrelets become gently swollen, whilst in specimens more than 60mm in length they are prominently swollen. As the bourrelets become more tumid, there is an increase in the number of small, densely packed tubercles that cover them.

(6) This swelling of the bourrelets results in a change in outline of the peristome. In small specimens it is smoothly oval in outline, but in larger specimens the peristome becomes sub-pentagonal.

(7) The peristome and periproct decrease in relative size. For instance, in *E. posterocrassa*, a specimen 22.5mm in length, the diameter of the peristome is about one quarter of the test width. For a specimen 47mm in length, however, the diameter is only one-sixth of the

test width. An incomplete specimen of width 55mm has a peristome only one-eighth of this dimension.

(8) Small and medium sized specimens of *E. posterocrassa* generally bear only a single large tubercle on the apical system. Large specimens (more than 60mm in length) may have four or five. In *E. gambierensis*, however, the smallest specimens have two or three tubercles, whilst the large ones possess up to ten.

The smallest known specimen of *E. ovulum* has a test length of 30.7mm and had only one genital pore weakly developed, indicating that the specimen had just reached sexual maturity. At a similar size, specimens of *E. gambierensis*, *E. morgani* Cotteau and *E. posterocrassa* Gregory all have well developed genital pores. Specimens of *E. posterocrassa* as small as 22mm in length possess genital pores, and so were presumably sexually mature. A specimen 12mm in length, however, has no genital pores developed. *E. ovulum* attained a larger size before the onset of maturity than did other Australian species of *Echinolampas*.

Discussion: It is possible to interpret some of the morphological changes which occurred with growth in terms of change in life habit. Kier (1962, p 2) has conjectured that cassiduloids lived partially buried in sediment to the base of the ambulacral petals. This interpretation was influenced by Agassiz's (1873, p 555) observation on the life habits of *Rhyncholampas pacificus* (Agassiz). Higgins (1974) has shown that the cassiduloid *Apatopygus recens* (Milne Edwards) burrows completely, which throws some doubt on Kier's generalization. Unfortunately data is lacking on the life habits of living species of *Echinolampas*. Several dead tests of *Echinolampas ovata* from Roebuck Bay, Western Australia which have been examined by one of us (K.J.M.) clearly show staining of the test above the level of the tips of the petals. This staining appears to have been made by algal growth on that part of the test projecting above the sediment. It would seem that at the time of death of the test at least, it was buried in the sediment only below the level of the distal tips of the petals. If, indeed, *Echinolampas* is oriented in the sediment like *Rhyncholampas*

(buried only below the petals) then the different lengths of the anterior and posterior petals means that the oral surface would have been inclined to the sediment/water interface (Fig. 6). The effect of this orientation would be to position the apical system at the highest point above the sediment, and directly above the peristome. Such tilting would also mean that the periproct and peristome would be at the same level beneath the surface of the sediment.

Thum and Allen (1976) have reported that in a very coarse shelly sediment, *Echinolampas crassa* (Bell) often burrows completely under laboratory conditions. However, the burrowing behaviour of echinoids is notoriously variable, depth of burrowing within a species varying with time of day, size, gonadal condition, rate of movement, nature of sediment, wave action and water temperature (Chesher 1969).

Species of *Echinolampas* are characterised by the irregular lengths of the poriferous tracts of the ambulacra. It is conceivable that at periods

when individuals were only partly buried, say at night or at times of spawning, the echinoid would not have been orientated with its oval surface horizontal, but with the ends of the poriferous tracts of the ambulacra lying along the sediment/water interface (Fig. 6).

In fact, during growth the adoral surface becomes more domed, but the adoral part of the test maintains its profile, so that the peristome remains buried to about the same depth in their natural habitat.

As mentioned above, there is considerable variation in the height of the test within some species. Specimens of *E. posterocrassa* from the Nanarup Limestone are flatter and specimens from Kangaroo Island more conical than those from the Tortachilla Limestone. Likewise specimens of *E. morgani* from the Mannum Formation may be more conical than topotypes from Mt. Gambier. A consistent correlation does exist, however, between the length of the petal and the height of the test, for those specimens with a lower test have shorter petals.

Figure 6— Suggested possible life orientations of juvenile and adult *Echinolampas posterocrassa* Gregory, x1.



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Explanation of plates

PLATE 1

Figs 1-6—*Echinolampas posterocrassa posterocrassa* Gregory, 1890, from the Tortachilla Limestone (Late Eocene) Port Willunga, South Australia; 1, enlargement, x10, of apical system of NMV P55448; 2, enlargement, x5, of peristome and floscelle of NMV P55450; 3, 4 and 6, NMV P55447; 5, NMV P55449.

Figs 7-9—*Echinolampas posterocrassa curtata* subsp. nov. from the Port Vincent Limestone (Late Oligocene), 4km north of Wool Bay, Yorke Peninsula, South Australia; NMV P55451, holotype; 9, enlargement, x5, of peristome and floscelle.

Figs 10-13—*Echinolampas morgani* Cotteau, 1889, NMV P55455, from the Mannum Formation (Early Miocene), Murray River cliffs; 10, enlargement, x6, of apical system.

Except where otherwise stated, figures are x1.

PLATE 2

Figs 1-3—*Echinolampas morgani* Cotteau, 1889; 1, enlargement, x5, of petal of ambulacrum V of NMV P55455, from the Mannum Formation (Early Miocene), Murray River cliffs; 2-3 NMV P19176 from the Gambier Limestone (Early Miocene), Mt. Gambier, South Australia; 3, enlargement, x4, of peristome and floscelle.

Figs 4-8—*Echinolampas ovulum* Laube, 1869, NMV P55457, neotype, from the Mannum Formation (Early Miocene), Blanchetown, South Australia; 7, enlargement, x5, of part of petal of ambulacrum I; 8, enlargement, x6, of peristome and floscelle.

Except where otherwise stated, figures are x1.

PLATE 3

Figs 1-7—*Echinolampas gambierensis* Tenison Woods, 1867; 1-3 AUGD S35, neotype, from the Gambier Limestone, Mt. Gambier, South Australia; 4, enlargement, x6, of apical system; 4-5 NMV P55463 from the Mannum Formation (Early Miocene), Murray River Cliffs; 6, enlargement x3.5, of peristome and floscelle of NMV P55461 from the Gambier Limestone, 1.5km north of Nelson, Victoria.

Figs 8-11—*Echinolampas tatei* Lambert, 1898 from the Fossil Bluff Sandstone (Longfordian, Early Miocene) at Table Cape, Tasmania; 8-10 AUGD T358, holotype; 11, enlargement, x8, of part of petal of ambulacrum I of NMV P55464.

Except where otherwise stated, figures are x1.

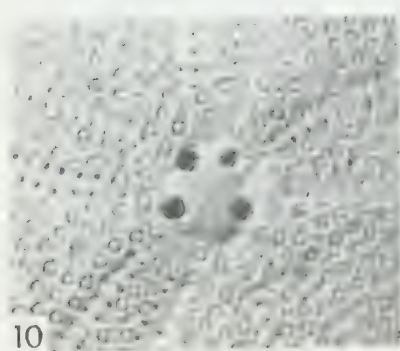
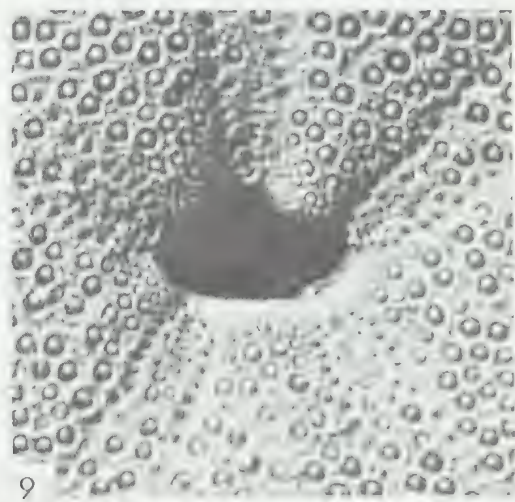
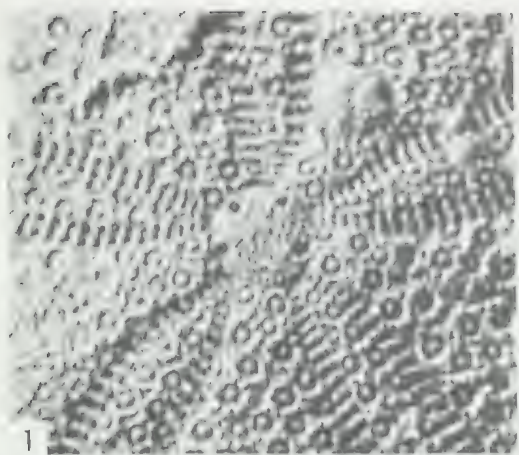
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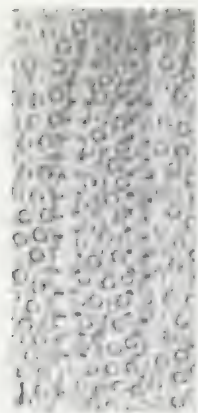
Figs 1-3—*Echinolampas* aff. *tatei* Lambert, 1898, NMV P55466, from the Gambier Limestone, left bank of Glenelg River, Nelson, Victoria.

Figs 4-6—*Echinolampas gregoryi gregoryi* sp. nov. NMV P18379, holotype from Orbost Victoria, probably Bairnsdale Limestone (Middle Miocene).

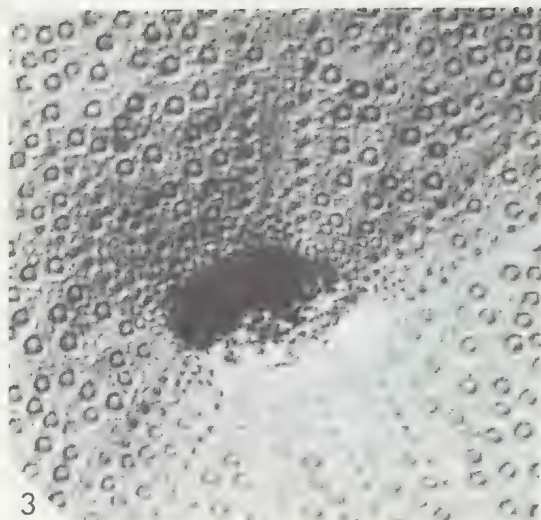
Figs 7-9—*Echinolampas gregoryi corrugata* subsp. nov. NMV P55477, from the Balcombian, Muddy Creek Formation (Middle Miocene) at Clifton Bank, Victoria.

All figures x1.

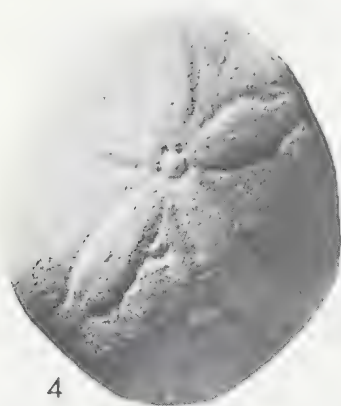




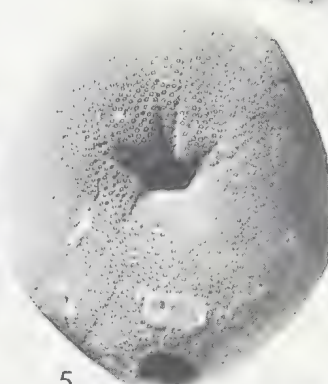
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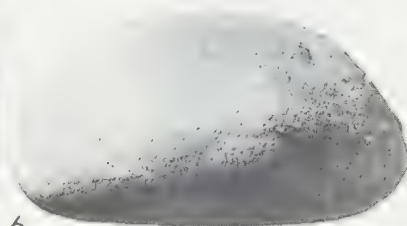
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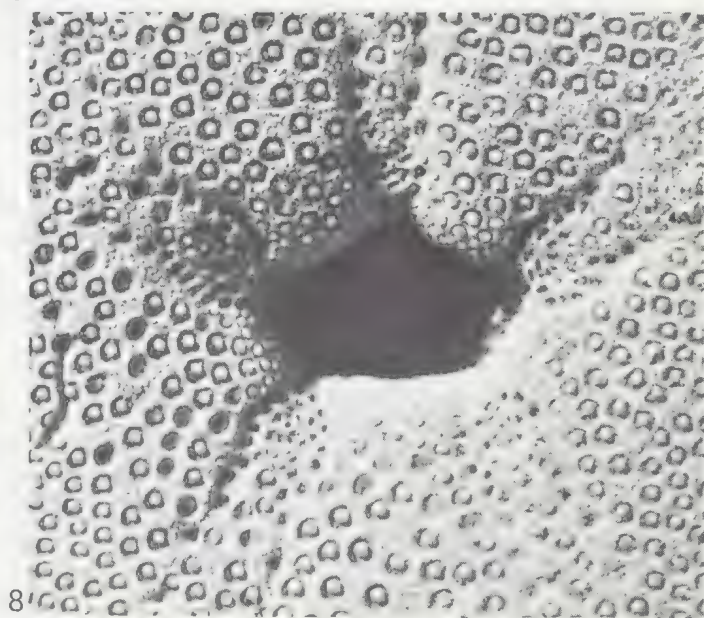
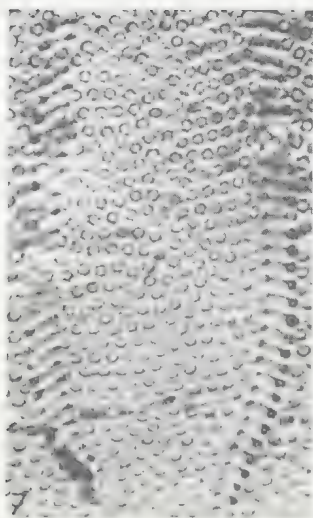
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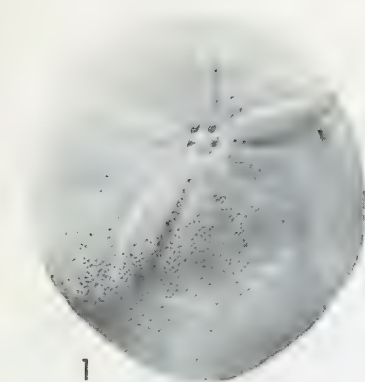
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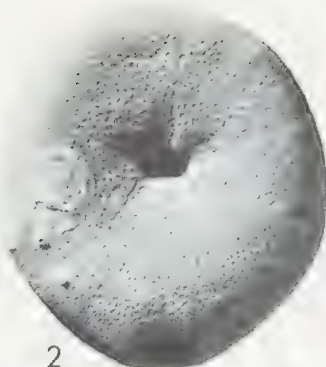
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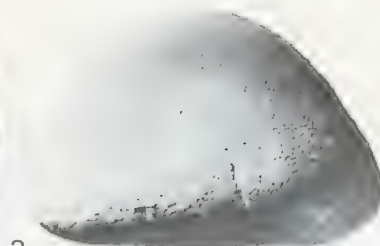
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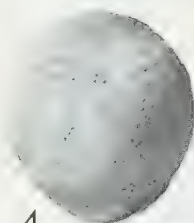
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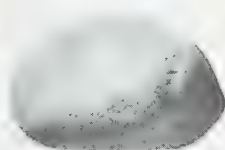
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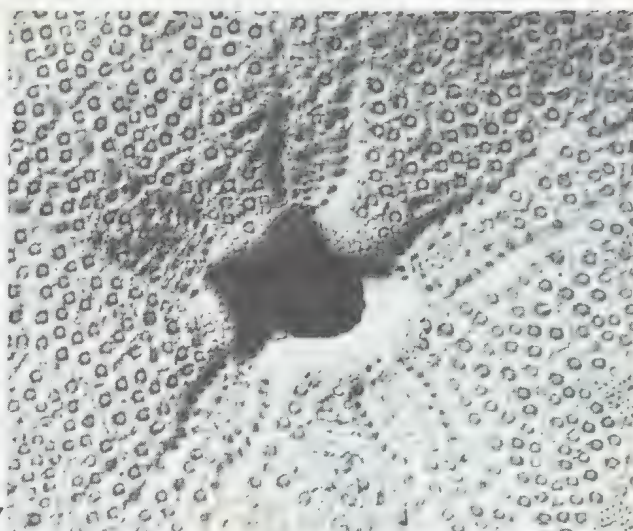
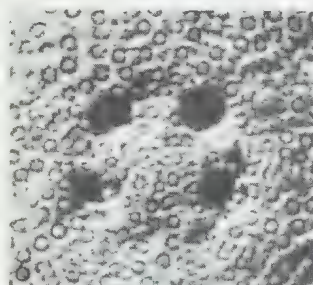
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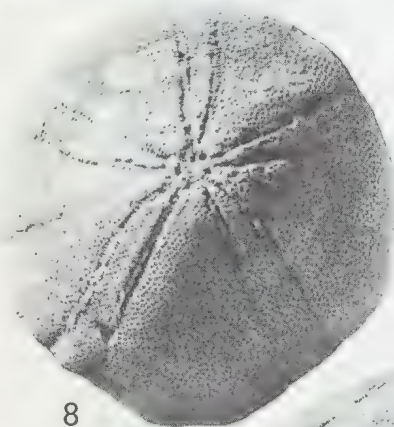
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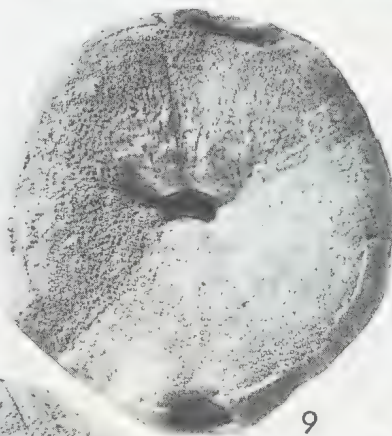
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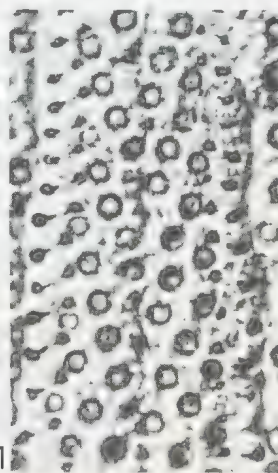


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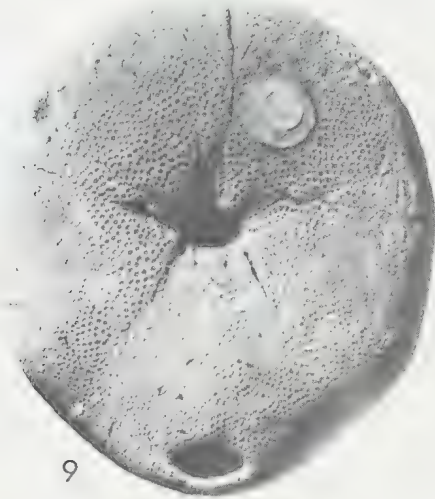
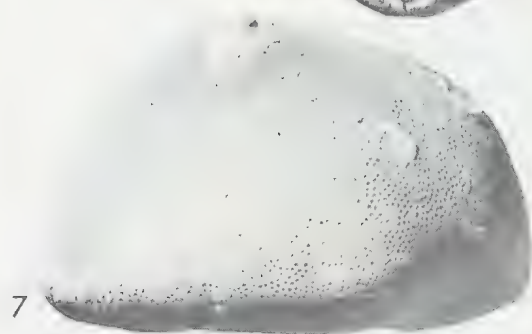
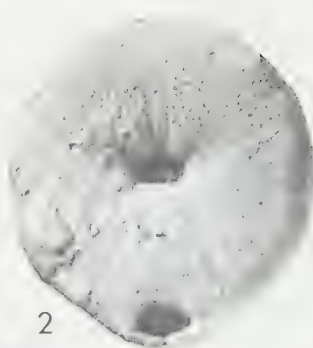


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SILURO-DEVONIAN NOTANOPLIIDAE (BRACHIOPODA)

By MICHAEL J. GARRATT

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Abstract

The Notanopliidae is reviewed and its systematic position is discussed. The family is divided into two subfamilies: Notanopliinae Gill, and Costanopliinae subfam. nov. Representatives of the family placed in the genera *Notoparmella*, *Notanoplia* and *Boucotia* from the Siluro-Devonian sequence of the Melbourne Trough are described. They are: *Notoparmella plentiensis* sp. nov., *Notanoplia panifica* sp. nov., *N. philipi* sp. nov., *N. pherista* Gill, *Boucotia janaea* sp. nov., *B. australis* (Gill), *B. withersi* (Gill), and *B. loyolensis* (Gill).

Introduction

Since Gill's (1969) work on the Notanopliidae, knowledge and number of constituent genera of the family have increased, from the two genera known then to some eleven genera. During a study of the brachiopod fauna of the Siluro-Devonian of the Melbourne Trough it became apparent that numerous representatives of the family are present, many of which are new. These are referred to the genera *Notoparmella*, *Notanoplia* and *Boucotia*. Further, the occurrence of previously described species is revised and consideration given to the phylogeny of the group.

The Siluro-Devonian stratigraphic succession of the Melbourne Trough has recently been reviewed by VandenBerg, Garratt and Spencer-Jones (1976). The lithostratigraphy and biostratigraphy of the Siluro-Devonian strata of the Melbourne Trough are described more fully elsewhere (Garratt, 1980, in prep.), and the stratigraphic sequence is not reviewed further here.

Collections

Registered number prefixes refer to the following institution:

NMVP—National Museum of Victoria.

MUGD—University of Melbourne Geology Department.

Terminology

The terminology described for the Notanopliidae follows that of Moore (1965) and Gill (1969).

Abbreviations

The following abbreviations used in the text are listed:

Hw	= Hinge width.
Mw	= Maximum width.
Lvv	= Length of the ventral valve measured from umbo to anterior commissure.
Ldv	= Length of the dorsal valve, measured from the cardinal process to the anterior commissure.
Lms	= Length of the median septum.
<ls	= angle between lateral septa.
<as ₁	= angle between inner accessory septa.
<as ₂	= angle between out accessory septa.
Wd	= Width of delthyrium.
Hd	= Height of delthyrium.

Suborder CHONETIDINA Muir-Wood 1955
Superfamily **PLICANOPLITACEA** superfam.
nov.

(= *Plicanopliacea* Xu Hankui 1977, p. 59).

Diagnosis: Small strophic impunctate shells with thin visceral cavity; ventral valve with pedicle tube but lacking a foramen, muscle scars indistinct; cardinal process recurved and rectangular with long axis transverse, socket ridges nearly parallel to the hingeline, brachidium possibly of ptycholophous lophophore. (New diagnosis)

Discussion: The superfamily Plicanopliacea and the family Plicanopliidae (sic.) were erected by Xu Hankui in March 1977, unfortunately based on *Plicanoplia* Havlicek (*non* Boucot and Harper, 1968). These familial names are invalid (I.C.Z.N., Article 39. a (i)). The group of brachiopods encompassed by Xu Hankui's Plicanopliacea, warrants (at least) superfamilial

status; hence the familial name Plicanoplitidae and superfamilial name Plicanoplitacea are proposed as replacement names based on the nominal genus *Plicanoplites* Havlicek, 1974.

Examination of Xu Hankui's excellent illustrations leaves no doubt as to the distinctive characters of *Paraplicanoplia* when compared with *Plicanoplites* (Havlicek, 1974) in such details as strength of external ribs and arrangement of the internal dorsal septa; (see Xu Hankui, table p. 64 and pl. 2, figs. 1-10, and pl. 3, figs. 14-20; cf. Havlicek 1973, pl. 1, figs. 1-9). The type species of *Paraplicanoplia* is *P. nana* Xu Hankui, 1977.

The generic name *Plicanoplia* was proposed by Boucot and Harper (1968, p. 169) for "coarsely costate anopliids with prominent accessory septa and anderidia in the brachial valve". The type species of *Plicanoplia*, Boucot and Harper is *Chonetes fornacula* Dunbar (1920, p. 130). The type species is well illustrated by Boucot and Harper (1968, p. 29, figs. 21-27; pl. 30, figs. 1-5). The genus clearly belongs to the chonetidine family Anopliidae, Muir-Wood (1962; *nom. trans.* Boucot and Harper 1968, p. 167 *ex* Anopliinae Muir-Wood 1962, p. 53).

Plicanoplia was again proposed as the name of a new genus by Havlicek (1973, p. 337) with *Plicanoplia peculiaris* Havlicek (1973) as type species. The genus was assigned to the Notanopliidae Gill, 1969. The diagnosis reads as follows: "Shell minute, subquadrate in outline, low, slightly convexo-concave in sagittal profile. Each valve bears two or more plicae of inconspicuous relief extending from the beak but dying out before reaching the front margin of the valve. Ventral interarea flat, apsacline medianly with an open delthyrium; dorsal interarea almost linear, anacline. Internal morphology of both valves same as that of *Notanoplia* Gill except for a sub-marginal rim well developed in the adult valves of the Bohemian genus" (Havlicek, 1973, p. 337-338).

As noted by Havlicek (1974, p. 170), *Plicanoplia* Boucot and Harper, and *Plicanoplia* Havlicek are homonyms (I.C.Z.N. Section 12, p. 51). *Plicanoplia* Boucot and Harper had priority; hence Havlicek's junior

homonym was replaced by the generic name *Plicanoplites* with *Plicanoplia peculiaris* Havlicek as type species.

It is noted that the genus *Imatrypa* (Havlicek, 1977, p. 300) published in September 1977, is probably a junior synonym of *Paraplicanoplia* Xu Hankui published in March 1977.

Two families are recognised: Plicanoplitidae fam. nov. and the Notanopliidae. The following genera are assigned to the Plicanoplitidae: *Paraplicanoplia* Xu Hankui, 1977 (= *Imatrypa* Havlicek, 1977); *Tangxiangia* Xu Hankui, 1977; and *Plicanoplites* Havlicek, 1974.

The generic assignments to the Notanopliidae are discussed under each of the two subfamilies.

Range: Late Silurian (?Ludlovian) to Middle Devonian.

Phylogeny Diagram: The applicability of the stage names for the Late Silurian-Early Devonian discussed elsewhere (Garratt, in prep.). Stages are shown as being of varying duration and reflect their number of graptolite and conodont zones rather than radioactive decay dates. These durations may well require alteration if and when radioactive decay dates become available.

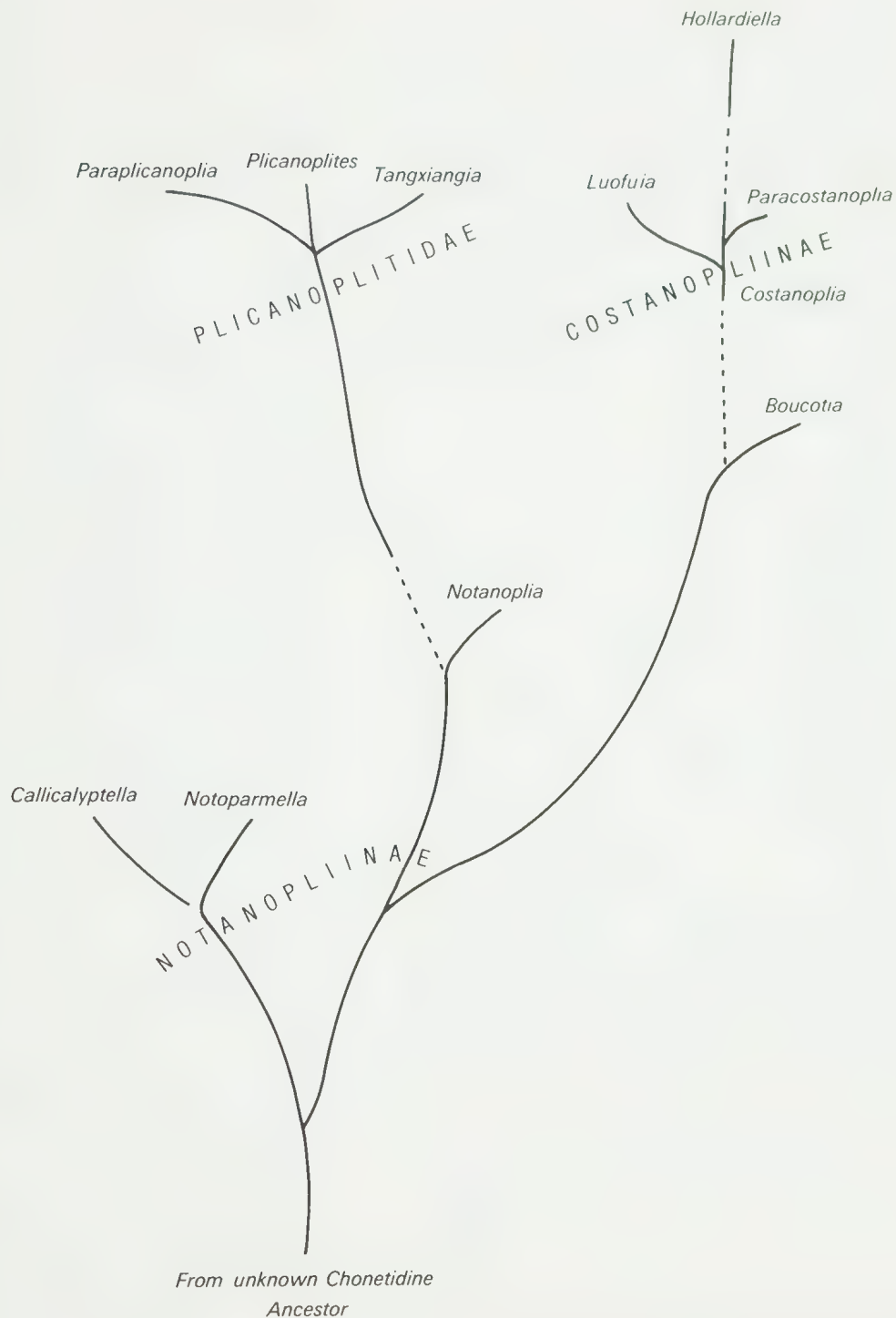
The diagrams (Figs) are dendritic in style and the branchlets do not necessarily indicate closeness of similarity time.

The proposed phylogeny and age ranges of the genera belonging to the Plicanoplitacea are shown in Fig. 1. The detailed morphology of the Notanopliidae is reviewed below. It is considered that the Plicanoplitacea includes two basic stocks here defined as families Notanopliidae and the Plicanoplitidae. One is characterised by a submarginal rim connecting the septa in the interior of the shell (Plicanoplitidae) the other lacks this structure (Notanopliidae).

The notanopliid stock arose, probably in the Late Silurian of south east Australia. Again two basic stocks are recognised separated from each other in space and time. These stocks are herein defined as subfamilies, one being essen-

Figure 1. Inferred phylogeny for the Plicanoplitacea.

LATE SILURIAN		EARLY DEVONIAN			MID. DEVONIAN
LUDLOVIAN	PRIDOLIAN	LOCHKOVIAN	PRAGUIAN	ZLICHOVIAN	EIFELIAN



tially characterised by smooth or finely costellate shells, the other by essentially costate shells. Variation in the number of lateral septa, from genus to genus, (noted also by Johnson, 1973, p. 1024), may be related to environmental factors and consequently similar gross internal morphologies developed in both stocks at different times. Examples of such convergent internal morphologies are: a distinct median septum in *Notoparmella*, a smooth or weakly costellate Late Silurian form, and in *Hollardiella*, a costate shell from the Late Eifelian; and a pair of divergent lateral septa and median septum in *Notanoplia*, a smooth or very weakly costate Early Devonian form and in *Costanoplia* a markedly costate, Middle Devonian genus.

The convergence of costation in the Notanopliidae is not so marked. Only the very rare genus *Callicalyptella* is markedly costate. Costate notanopliids are otherwise confined to the Middle Devonian.

Notanoplia arose from *Notoparmella* probably in the Late Silurian by development of a pair of smooth lateral septa. *Boucotia* arose from *Notanoplia* by further modification of the septa into crested speta. The basic Plicanoplitid stock represented by *Plicanoplites* probably arose from either *Notanoplia* or *Boucotia* during the Praguian. The presence of *Notanoplia* in Siegenian strata of Germany (Langenstrassen, 1972, p. 49) and its close temporal proximity to the first occurrence of *Plicanoplites* from the Dvorce Limestones (Zlichovian) of Bohemia (Havlicek, 1973) supports an origin of the Plicanoplitidae via *Notanoplia*. I am unaware of any record of *Boucotia* from the Early Devonian of central Europe.

Family NOTANOPLIIDAE Gill, 1969

(emend. Boucot and Johnson, 1972, p. 299, and Savage, 1974, p. 20, emend. herein).

Diagnosis: Small plano-convex or convavo-convex brachiopods with a straight hingeline and variably developed ventral interarea; shell surface smooth or costate; interiors with unequal or equal number of lateral septa or com-

pletely lacking lateral septa; ventral teeth are large, simple and deltodont (new diagnosis).

Discussion: The Notanopliidae have been variously classified as chonetids (Gill, 1942, 1945a, 1950), leptestiids (Philip, 1962; Langenstrassen, 1972; Savage, 1974), atrypaeans (Johnson, 1973; Havlicek, 1973, 1974, 1977; Gratsianova and Schischkina, 1977) or incerta cedis (Gill, 1969; Boucot and Johnson, 1972).

Gill (1950) argued for a close affinity of *Notanoplia* with *Anoplia* Hall & Clarke of the chonetidine family, Anopliidae, on the basis of similarity of shell shape, internal septa and the isochronous development with *Anoplia*.

Philip (1962, p. 206) proposed a leptestiid assignment for *Notanoplia*. This assignment was based on the absence of spines and spine bases along the edge of the ventral interarea of *Notanoplia*, the presence of strong divergent socket ridges and a suggestion of a trilobed cardinal process in *Notanoplia*. This plectambonitacean assignment was accepted by Langenstrassen (1972, p. 49) and tentatively by Savage (1974, p. 27).

Gill (1969) placed the family Notanopliidae under incerta cedis. His reasons (p. 1230) were based on internal structures—the lateral and median septa of both valves and the unique scroll-like cardinal process of the Notanopliidae. He noted the similarity of outline of the Notanopliidae to the Chonetidina but stated that anderidea (Sadlick, 1965) and hinge spines are lacking.

However, Johnson (1973), Havlicek (1973, 1974, 1977) and Gratsianova and Schischkina (1977) attributed the Notanopliidae to the Atrypacea, arising from either the Anoplithecidae (Havlicek, 1973, p. 337) or the Carinatininae (Johnson, 1973, p. 1026). Johnson's reasons for an atrypacean assignment were based on:

(i) similar impunctate shell structure of Notanopliidae and Atrypacea;

(ii) the carinatinid genus *Gracianella* Boucot and Johnson and the notanopliid *Hollardiella* Drot, both have simple socket plates, solid transverse cardinal process and a short thick dorsal median septum.

(iii) the similarity of shape, smooth shells and presence of a median rib in the dorsal valve of *Notoparmella* Johnson and *Gracianella* (Johnson, 1973, p. 1025).

Havlicek (1973, p. 337) suggested that "the peculiar cardinal process of the notanopliid genera may represent a composite structure originated by the fusing of the hinge plates and cardinal process into one body and to some extent recalling the hinge morphology of some brachiopods of the family Anoplithecidae".

The dichotomy of opinion concerning an adequate superfamily assignment for the Notanopliidae, prompted Xu Hankui (1977) to raise them to superfamily status. This status is accepted but the problem of their ordinal affinities and origin remain.

I consider that the strophic shell of Notanopliidae (and the Plicanoplitidae) and the possession of lateral septa reflect an affinity and origin with the Chonetidina (with loss of hinge spines and pseudopunctae) rather than the Atrypidina for the following reasons:

(i) All genera belonging to the Plicanoplitacea have strophic shells, with either a low or linear ventral interarea (i.e. they have a straight hingeline). Not one Late Silurian atrypide genus has a straight hingeline, all are curved albeit if some are gently so, and are therefore, non-strophic shells. It should be noted that only the late Early Devonian carinatinid genera *Biconostrophia* Havlicek, 1956, *Prodauidsonia* Havlicek, 1956, *Davidsoniatrypa* Lenz 1968, *Carinatinella* Gratsianova 1967, and *Carinata* Nalivkin, 1930, have a straight hingeline, but this is a modification which is only attained in the adult or gerontic stages as typified by *Biconostrophia* (Johnson and Boucot, 1972, p. 35).

They are essentially non-strophic shells. Further, non-strophic shells are diagnostic of the Rhynchonellida. Copper (1967a, 1967b,) argued that the atrypide stock arose from the Rhynchonellida because both groups had basic similar umbonal ventral and dorsal structures. It seems plausible that the similarity in the internal organisation of those structures can also be inferred by their common form; i.e. their non-strophic outline.

Johnson and Boucot's (1972) concept of the

Carinatininae includes *Dnestrina* Nikiforova and Modzalevskaya 1968. Their illustrations of the internals (pl. 3, figs. 38, 39) of *D. gutta* Nikiforova and Modzalevskaya, the type species of *Dnestrina*, show cardinalia unlike those of other carinatinids. They recall the Notanopliidae except for a further modification of the cardinal process. *Dnestrina* is a non-strophic form which may not reside in the Carinatininae because all other genera assigned to the Carinatininae, including *Gracianella* Johnson and Boucot, have cardinalia unlike those of the Notanopliidae. Copper (1973a, p. 486, 1973b, p. 121) regards *Dnestrina* as a dayiacean athridid.

Johnson (1973, text fig. 2, p. 1023) further emphasized an atrypide affinity through *Gracianella*. Again few of the species of *Gracianella* have internal umbonal features of the shell which are similar to the Notanopliidae. Certainly Johnson's (1973) illustrations of *Notoparmella* (pl. 4, fig. 2, 7) compare with Johnson and Boucot's (1967, pl. 109, figs. 22, 23, 39, 40) illustration of *Gracianella Lissumbra* Johnson and Boucot; but see illustrations of *Gracianella plicumbra* Johnson and Boucot (1972, pl. 3, figs. 24-6). Nevertheless all species of *Gracianella* have a curved hingeline. *Gracianella* lacks the solid transverse structure of *Notoparmella* as illustrated by Johnson (1973, pl. 14, figs. 2, 12). Rather, the variation of cardinalia of *N. gilli* may perhaps be the result of incomplete silicification.

(ii) Similarities in shell structure between atrypides and plicanoplitaceans may be fortuitous. Johnson, (1973, p. 1025) laid great emphasis on the absence of punctae and pseudopunctae in the silicified material of *Notoparmella gilli*, the nonsilicified shells of *Hollardiella*, and the absence of pits in well preserved internal moulds of *Notanoplia*, *Boucotia* and *Callicaltptyella*; drawing the conclusion that all the members of the Plicanoplitacea are impunctate. He may well be correct, but silicification normally destroys shell structure and internal moulds of Notanopliidae are smooth. *Notanoplia philipi* sp. nov. has perforations in the lateral septa which may be pseudopunctae (pl. 7, fig. 1). One specimen of *Notoparmella plentiensis* sp. nov. has perforations in the

anterior portion of the median septum. Their regular spacing and outline preclude these perforations from being produced from borers. These perforations are considered remnants of pseudopunctae.

(iii) The arrangement of the lateral, accessory and median septa of the (Para) Plicanoplitacea are similar to those characterising the Chonetidina. Gill (1945, 1950) accepted chonetide affinity of the Notanopliidae but later (1969, p. 1223) drew a distinction between lateral septa (Muir-Wood, 1962) = anderidia (Sadlick 1965, p. 157-9), accessory septa and median septa of the Chonetacea and the septal configuration of the Notanopliidae. In terms of their functional morphology, Gill (1969, p. 1228) suggested that the lateral septa of notanopliids functioned as controllers of exhalant and inhalant currents and for placement of organs. Grant (1976, p. 65 Text Fig. 11) postulated that the chonetacean lateral septa served as a seat for a ptychophorous (or complex schizolophe) lophophore. It seems plausible that the lateral septa of plicanopliaceans also functioned in the same way. No other structures are preserved or hinted at in the dorsal valve which could have supported the lophophore. I suggest that the septa of the plicanopliaceans functioned as lophophore supports and that they are homologous with those of the Chonestacea.

In deriving the Plicanoplitacea from the Chonetacea the latter have to lose pseudopunctae hinge spines, denticulate hinge, a chilidium and pseudodeltidium.

Finally a plectambonitacean origin for the Plicanoplitacea cannot be entirely discounted, but they too have to lose a denticulate hinge, pseudodeltidium, chilidium and pseudopunctae.

Subfamily COSTANOPLIINAE subfam. nov.

Diagnosis: Notanopliids with a costate shell or rarely smooth.

Discussion: Genera assigned include: *Costanoplia* Xu Hankui; *Paracostanoplia* Xu Hankui; *Hollardiella* Drot; and *Luofuia* Xu Hankui.

The Costanopliinae first appear in Late Zlichovian to Early Eifelian of southwest China. There are no known costanopliinids known from older strata but it is suggested herein that the subfamily probably arose from *Boucotia*, a widely distributed genus, rather than from the plicanopliid genus *Plicanopliites*. This is because the distinctive raised rim in the internal dorsal and ventral valve of the Plicanopliitidae is absent in the Notanopliinae.

Range: Late Zlichovian to Late Eifelian (Devonian).

Occurrence: The Costanopliinae are found in the late Eifelian of Morocco (Drot, 1967) and the late Zlichovian-Early Eifelian of southwest China.

Subfamily NOTANOPLIINAE Gill, 1969
(nom. trans. ex. Notanopliidae Gill (1969, p. 1223))

Diagnosis: Notanopliids with a smooth exterior or fine costellae rarely costate.

Discussion: The Late Silurian to Early Devonian notanopliids are smooth (*Boucotia*) or have very fine ill-developed costellae (*Notanoplia*, *Notoparmella*) or are costate (*Callicalpytella*). *Callicalpytella*, although costate appears to be more closely related to *Notoparmella* because of its close juxtaposition in space and time and similar outline. (Fig. 2).

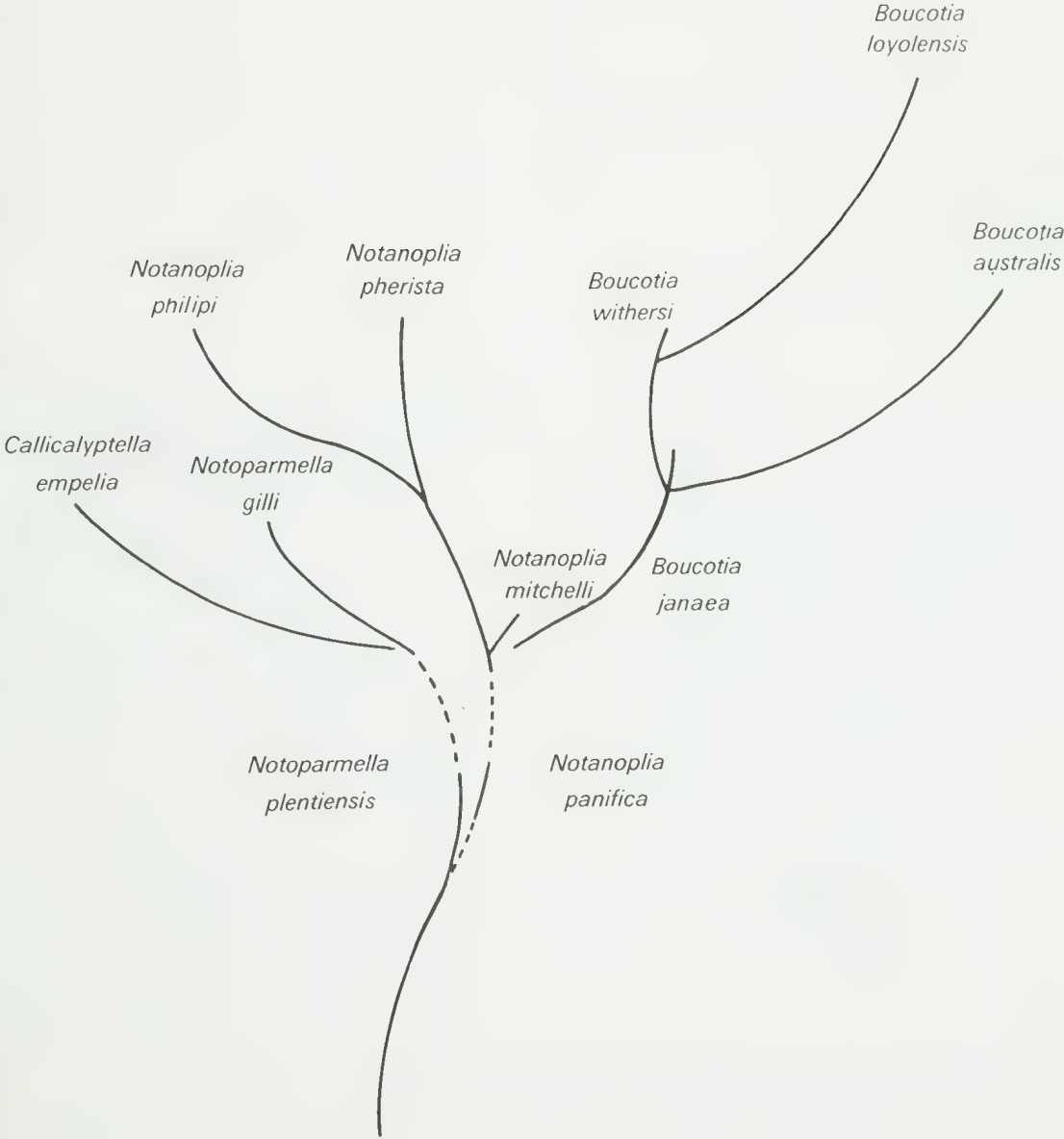
Genus *Notoparmella* Johnson, 1973

Type species: *Notoparmella gilli* Johnson, 1973, p. 1026-7, pl. 4, figs. 1-17, pl. 5, figs. 4, 5.

Diagnosis: A small thin shelled, shield shaped, concavo-convex or plano-convex notanopliid, with variably developed fine costellae or apparently smooth, except for a ventral median fold. Interiors with impressed ventral diductors and simple discrete socket plates, variably strengthened by deposit of shell material into a

Figure 2. Inferred lineage for Notanopliidae.

SILURIAN		DEVONIAN	
LUDLOVIAN		PRIDOLIAN	LOCHKOVIAN
		PRAGUIAN	ZLICHOVIAN



- 1 *Notoparmella*
- 2 *Notanoplia*
- 3 *Boucotia*
- 4 *Callicalyptella*



Figure 3. Distribution of the Notanopliidae.

single transverse bar. Ventral median septum varyingly developed (new diagnosis).

Discussion: Johnson's (1973, p. 1026) diagnosis is emended to include reference to costellae. *Notoparmella plentiensis* sp. nov. is invariably costellate but has identical internal characters to *N. gilli* from Windmill Limestone of Coal Canyon, Nevada (Lochkovian). Absence of lateral septa in the ventral and dorsal interiors of *Notoparmella*, distinguished it from *Notanoplia*, *Boucotia*, and the rare genus *Callicalyptella*.

Range: Late Silurian (?Ludlovian) to Early Devonian (Lochkovian).

***Notoparmella plentiensis* sp. nov.**
(Plate 5, figs. 1-27; plate 6, figs. 1-3)

Derivation of name: After the hamlet of Plenty.

Holotype: Specimen NMVP 49695 which is an internal mould of an articulated specimen, and is illustrated pl. 5, figs. 1, 2 herein.

Paratypes: NMV P49601, NMV P49603-4, NMV P49607-8, NMV P49610, NMV

P49613-14, NMV P49616, NVM P49625, NMV P49628, NMV P49637, NMV P49641-2, NMV P49644, NMV P49647, NMV P49652, NMV P49664, NMV P49666, NMV P49674, NMV P49697, NMV P49699.

Figured Specimens: NMV P496750 & b, NMV P49751.

Type locality: Locality A17, a small road cutting on the west side of the Whittlesea-Plenty Road. Coords. 104800 Kinglake 1:50,000 Military map.

Type strata: Humevale Formation.

Material: A total of 121 specimens comprising 25 external and 51 internal moulds of the ventral valve and 21 external and 24 internal moulds of the dorsal valve from the type locality. The high ratio of dorsal to ventral valves suggests sorting prior to deposition.

Description: Exterior: The valves are small, not exceeding 7.2 mm in width and 5.5 mm in length. They are semicircular in outline and plano-convex, more rarely concavo-convex in lateral profile. The hingeline is straight and is usually equal to the maximum width of the

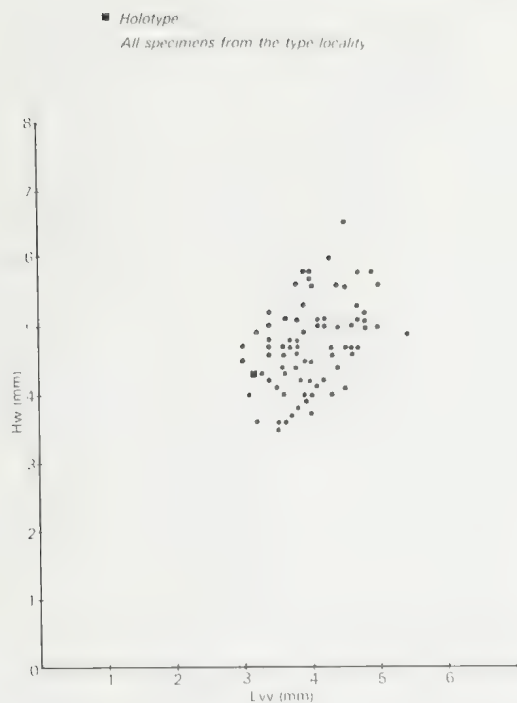


Figure 4. Scatter diagram of Hw:Lvv *Notoparmella plentiensis* sp. nov.

shell. A low apsacline area is developed in the ventral valve which is interpreted as a ventral interarea. It either extends to the cardinal extremities of the shell as a low ridge or terminates two thirds of the distance to the cardinal extremities of the valve. The dorsal posterior margin is linear. The ventral valve is gently to highly convex, the median portion being modified by the development of a median furrow. The dorsal valves bear a broad ill-defined sulcus which fades laterally into the flanks of the valve. The dorsal valve bears a median narrow costella, originating anterior to the umbo and extending to the anterior commissure.

The exterior of the shell is finely costellate (pl. 5, figs. 5, 8, 11) with the costellae increasing anteriorly by intercalation.

Interior of the ventral valve: The hinge teeth are relatively large and formed without any development of ventral adminicula. They are widely divergent and project beyond the hingeline. The delthyrium is triangular and



Figure 5. Scatter diagram of Hw:Ldv *Notoparmella plentiensis* sp. nov.

wide. The posterior portion of the floor of the cavity is sculptured by a triangular diductor muscle field (pl. 5, figs. 16, 19). In larger specimens the muscle scar is deeply impressed and extends anterolaterally for one third of the distance to the commissure, where its width is equal to two thirds of the width of the valve at this position. The posterior angle of the postero-lateral borders of the muscle field is approximately 90°. The interior is smooth apart from a median septa which originates a short distance from the ventral diductor field and bifurcates at approximately three-quarters of the length of the valve. The anterior rim of the valve is sculptured by grooves which probably reflect the position of setae in life.

Interior of the dorsal valve: The sockets are shallow and widely divergent. They are defined by short divergent socket ridges originating from the apex of the notothyrium. The socket plates fuse posteriorly to form a transverse structure that curves around posteriorly

duplicating the scroll-like cardinal structure of *Notanoplia*, *Boucotia* and *Callicalyptella*.

A well-defined, low dorsal median septum originates anterior to the scroll-like cardinalia (the cardinal plate of Boucot and Johnson, 1972, p. 392) and bifurcates three-quarters of the distance to the anterior commissure. The interior is smooth except for the faint impressions formed by costellae adjacent to the anterior commissure.

Discussion: The high convex ventral valve well developed ventral median septum and the costation of the shell serve to distinguish *Notoparmella plentiensis* sp. nov. from the type species *N. gilli*. *N. plentiensis* is the oldest notanopliid found to date. It is associated with *Gracianella* and *Plectodonta bipartita* and occurs in rocks overly strata containing *Bohemograptus bohemicus* by 100 m at Plenty. Accordingly probably Ludlovian in age.

Occurrence: Localities A15 and A17 coords. 095812 and 103,803 Kinglake 1:50,000 Military map, near Plenty, and loc. W78 coords. 507865 Glenburn 1:50,000 Military map, Glenburn, Victoria of the Humevale Formation, which may be Pridolian or Lochkovian in age. Also occasionally at Pl. 260 in the Upper Dargile beds of Christmas Hills, coords 325562 Yan Yean 1:63360 Military map, which are probably Pridolian.

Range: Late Silurian (Ludlovian to ? Pridolian) to ? Early Devonian (Lochkovian).

Genus *Notanoplia* Gill, 1951a

Type species: *Notanoplia pherista* Gill, 1951a, p. 250-252, pl. 1, figs. 29-32.

Diagnosis: Notanopliinids lacking crested septa, i.e. with smooth septa. Exterior smooth or rarely ornamented with fine costellae.

Discussion: Gill (1969, p. 1226) clarified the generic diagnosis of *Notanoplia*. He recognised that the morphology of the septa in the ventral and dorsal valves of *Notanoplia* contrasted with those of *Boucotia australis* (Gill), *B.*

withersi (Gill) and *B. loyolensis* (Gill), which he had earlier assigned to *Notanoplia*, by these latter species having crested septa. This distinction was well illustrated by him. [See illustrations of *N. pherista* (Gill, 1969, pl. 143, figs. 1, 2, 5, 6) with those of *Boucotia australis* (pl. 143, figs. 9, pl. 143, figs. 8, 10) and *B. loyolensis* (pl. 144, figs. 19, 21)]. Illustrations of *B. withersi* do not show the crested septa but examination of Gill's hypotypes confirms their presence.

The generic distinction of *Notanoplia* from *Boucotia* is supported herein, even though considerable variation in the arrangement and morphology of the median and lateral septa occur in both genera. Smooth specimens of *Notanoplia* and *Boucotia* are homoeomorphic.

Notanoplia is almost entirely restricted to the Early Devonian of south eastern Australia. Only *N. panifica* sp. nov. is known from pre-Devonian deposits.

Three species are recognised: (1) *N. panifica* sp. nov. from the upper Dargile Formation of Christmas Hills, Victoria (? Late Ludlovian-Pridolian) is the only Silurian species known; (2) *N. pherista* from widely scattered localities of the Lochkovian to Praguian of south eastern Australia; and (3) *N. philipi* sp. nov. from Lilydale and Tyers, Victoria (late Lochkovian).

Species rejected from Notanoplia

Gratsianova (1967, p. 18, 52-54, pl. 3, figs. 17-19) described a form as *Notanoplia ganiensis* Gratsianova from the lower Devonian of the Horn Mountains near Kamishenko, Siberia, U.S.S.R. However, her illustrations show that it has well developed ears, a smooth exterior, high convex ventral valve and very short lateral and median septa. This assignment to *Notanoplia* is not accepted; the species probably merits erection of a new genus of the Anopliidae.

Species questionably assigned to Notanoplia

Langenstrassen (1972, p. 52, pl. 3 fig. 11) described *Notanoplia* sp. from the Rhenish lower Devonian of Germany (Siegenian). External of this species are unknown but it probably belongs to *Notanoplia*.

Xu (1979, p. 379) recorded *Notanoplia* from the lower Devonian (Siegenian) of north east

Dimensions of some specimens in mm

Specimen Number	Hw	Mw	Lvv	Ldv	(v) Lms	(d) Lms	(v) <ls	(d) <ls	Wd	Hd	costellae per mm
NMV P14827	11.1	11.1	7.1		5.8		105°		3.1	1.0	
NMV P14828	8.0	8.0		9.7		6.0		90°			
NMV P25557	6.6	9.6	8.1		5.8		90°				
NMV P25559	7.8	8.6	7.4		6.2		90°				
NMV P25561	6.0	6.0	8.4		7.4		80°				6
NMV P25562	9.4	10.1	8.2		8.0		90°				
NMV P25563	7.6	9.8	6.1		4.6		100°				
NMV P25564	5.7	7.7		7.9							
NMV P49721	3.1	4.4	2.8		2.1		90°				
NMV P49722a & b	6.5	7.2	5.0		5.0		90°				
NMV P14790	5.8	6.1	5.3								7-8

China, but no illustration or description of this species is known.

Notanoplia pherista Gill, 1951a

(Plate 6, figs. 1-18)

Synonymy:

- 1945 *Notanoplia australis* (Gill)—Gill, p1. VIII, fig. 4.
 1951a *Notanoplia pherista* Gill, p. 250-252 pl. 1, figs. 29-32.
 1969 *Notanoplia pherista* Gill—Gill, p. 1226-7 pl. 143, figs. 8 (*non* figs. 1-7), pl. 144, figs. 22-23.
 1974 *Notanoplia pherista* Gill—Savage, p. 27-28 pl. 6, figs. 1-20, Text figs. 10A, B.

Holotype: Specimen NMV P14827, which is an internal mould of the ventral valve; described and illustrated by Gill (1951a, p. 250-1, pl. 1, figs. 29, 30).

Paratype: Specimen NMV P14828a, which is an internal mould of the dorsal valve, described and illustrated by Gill (1951a, p. 251, pl. 1, fig. 31).

Figured Specimens: NMV P14790, NMV P14827b, NMV P5557, NMV P25559, NMV P25561-4, NMV P49721 and NMV P49722a & b.

Diagnosis: Notanopliinids lacking crested septa in both valves; external ornament fine costellate or smooth.

Type locality: Right bank of the Little Henty River, 1.5 km south east of Zeehan, Tasmania; loc. 16 of Gill (1951a, p. 250).

Type Strata: Bell Shale (Early Devonian).

Material: A total of 16 individuals are known from the type locality, including 9 internal moulds of the ventral valve, 5 internal and 2 ex-



Figure 6. Scatter diagram of Hw:Lvv for *Notanoplia pherista* Gill.

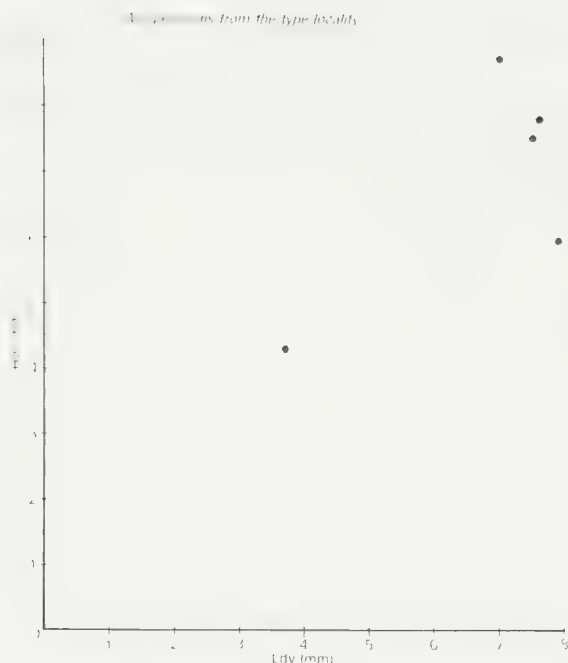


Figure 7. Scatter diagram of Hw:Ldv for *Notanoplia pherista* Gill.

ternal moulds of the dorsal valve. This description is augmented by 4 specimens from Kinglake, including two internal moulds and one external mould of the ventral valve and one internal mould of an articulated specimen.

Occurrence: *N. pherista* is an occasional species of the benthos of the Bell Shale of Tasmania. It is rare in the Humevale Formation of the Kinglake district and occasional in the Maradana Shale of New South Wales.

Description: Savage (1974, p. 27, 28) fully described *N. pherista* from the Maradana Shale, Manildra, N.S.W. Examination of all known topotypes from loc. 16, Bell Shale of Zeehan, Tasmania shows that the species is variable in outline and in external ornamentation.

Exterior: Some of the topotype material is smooth, with concentric growth lines as in NMV P14790 (p1. 6, fig. 6) or faintly costellate as in NMV P25561. The outline is more transverse in the holotype NMV P14827 with

maximum width of 11.1 mm at the hingeline and 7.1 mm in length. The Manildra material is commonly shield shaped.

- **Interior of the ventral valve:** No bifurcation of the median septum occurs in the type material but two specimens NMV P25559 and NMV P25563 show incipient development of accessory septa in the anterior portion of the valve between the median and lateral septa (p1. 6, figs. 10, 17).

Interior of the dorsal valve: Dorsal valves of the material from Manildra and Zeehan are identical.

Discussion: *N. pherista* has a variable external ornament but is never costate as in *N. philipi* sp. nov. *N. pherista* differs from *N. panifica* sp. nov. by its larger size and the latter has indistinct lateral septa, and is markedly costellate. *N. pherista* is easily distinguished from its external homeomorph *Boucotia australis* by lacking pitted lateral septa.

Range: Early Devonian (Lochkovian).

Notanoplia panifica sp. nov.
(Plate 6, figs. 19-26)

Holotype: NMV P49746 which is an internal mould of the ventral valve and illustrated on p1. 6, fig. 19 herein.

Paratypes: NMV P49475, NMV P49747a & b, NMV P49748a & b, NMV P49753, NMV P49754.

Type locality: P1. 260 east side of wall of Sugarloaf Reservoir, Christmas Hills, Victoria.

Type strata: Top of the Dargile Formation (? Late Ludlovian or Pridolian).

Derivation of name: From the latin *panifica* meaning loaf, after the name of the type locality.

Material: Six specimens including two internal moulds of the ventral valve and two internal and external moulds of the dorsal valve.

Dimensions of some specimens of *N. panifica* sp. nov.

Registered Number	Hw	Mw	Lvv	Ldv	(v) Lms	(v) <ms	(d) Lms	(d) <ms	costellae per mm
NMVP 49745	5.4	6.3	5.4		3.7	90°			6
NMVP 49746	4.6	5.8	4.9		3.6	90°			6
NMVP 49747A	5.5	7.0		4.6			2.5	105°	6
NMVP 49747B	5.5	7.0		4.6					
NMVP 49753	5.4	7.0	6.0		5.0	80°			
NMVP 49754	5.1	5.6		4.3					6

Diagnosis: *Notanoplia* with incipient lateral septa with a costellate external ornament.

Description: Shells are small, subquadrate in outline and plano-convex in lateral profile. The hingeline is straight with maximum width anterior to it. The exterior of the shell is costellate with six costellae per mm as measured at the anterior commissure.

Interior of the ventral valve: Hinge teeth are of average size for the genus and widely divergent. The delthyrial cavity is bounded by incipient lateral septa. These septa diverge anterolaterally between 80 and 90°. A strong median septum arises anterior to the apex of the delthyrial cavity and extends almost to the anterior commissure.

Interior of the dorsal valve: This is based on two dorsal valves, paratypes NMV P49747b and NMV P49748a. The median septum and faintly developed lateral septa originate anterior to the position occupied by the cardinal process—not preserved, and terminate abruptly about 1 mm from the anterior commissure. No pits are present on the septa.

Discussion: The earliest known *Notanoplia*, *N. panifica* is distinguished from *N. phillipi*, and *N. pherista* by its finer costellae and faint lateral septa.

Occurrence: *N. panifica* sp. nov. is presently known only from the type locality.

***Notanoplia philipi* sp. nov.**

(Plate 6, figs. 27-32, plate 7, figs. 1-10, 17, 33)

Synonymy:

1962 *Notanoplia* sp.—Philip, p. 208-9, pl. 31, figs. 11-17, Text fig. 13b, c.

1969 *Boucotia* sp.—Gill, p. 1227.

Diagnosis: *Notanoplia* with well developed costae on the surface of the shell, and no accessory septa.

Derivation of name: In honour of Professor Graeme Philip.

Holotype: Specimen MUGD 3441a which is an internal mould of the ventral valve and illustrated by Philip (1962, pl. XXXI, fig.).

Paratypes: MUGD 3441b, MUGD 3443, MUGD 3444.

Figured specimens: MUGD 3440, NMV - P49718A, NMV P49718B, NMV P49720, NMV P25489, NMV P49723, NMV P49724, NMV P25493-4, NMV P25535, NMV P25539 and NMV P25542.

Type locality: Locality 43, Parish of Boola, near Tyers, Gippsland, of Philip (1962).

Type strata: Boola Formation.

Material: A total of 10 specimens comprising 1 external and 7 internal moulds of the ventral valve and 2 internal moulds of the dorsal valve from the type locality. Specimens are known from Lilydale including 9 external moulds and

Dimensions of some specimens of *Notanoplia philipi* sp. nov.

Registered Number	Hw	Mw	Lvv	Ldv	(v) Lms	(v) < Ls	(d) Lms	(d) < Ls	costellae per mm
MUGD 3440	5.4	5.8		4.4			4.1	100°	5
MUGD 3441a	7.2	8.1	5.8		5.5	90°			4
MUGD 3441b	5.8	6.1	5.3		5.0	80°			5
MUGD 3444	6.4	7.5	6.1		5.7	100°			5
MNVP 49718a	5.0	5.4			4.1	95°			5
MNVP 49718b	5.0	5.4	4.4						5
NMVP 49720	5.8	6.0	5.2						5
NMVP 49723	1.5	1.8	2.1	2.1					4
NMVP 49724	4.5	4.6		4.0					4
NMVP 25489	4.3	4.3		3.7					5

The latter 4 specimens are from loc. 87 Lilydale, Victoria.

one internal mould of the dorsal valve and one external mould of an articulated specimen.

Description: Exterior: The shells are small subequal in length and width, not exceeding 9 mm in width. They are subquadrate to shield-shaped in outline, and concavo-convex in

lateral profile. The hingeline is straight with the maximum width anterior to the hingeline, situated about midlength of the shell and exceeding length. A low apsacline ventral interarea occurs on either side of the delthyrium and abruptly terminates half the distance to the cardinal extremities of the valve. The dorsal

- Specimens from locality 43, Boola Beds, Tyers
- Specimens from locality 87, Lilydale

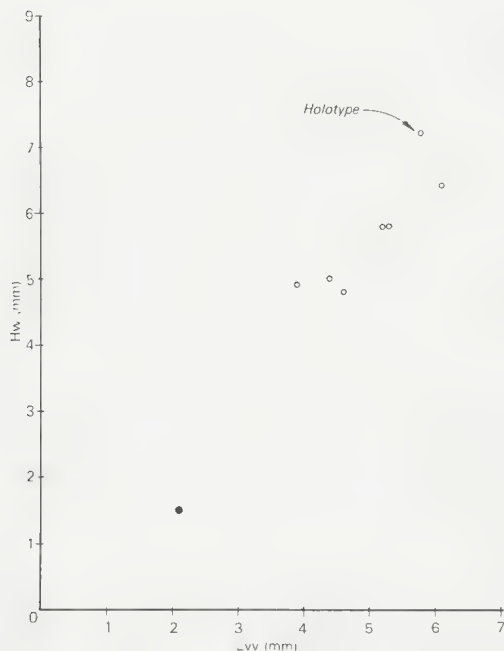


Figure 8. Scatter diagram of Hw:Lvv for *Notanoplia philipi* sp. nov.

- Specimens from locality 43, Boola Beds, Tyers
- Specimens from locality 87, Lilydale

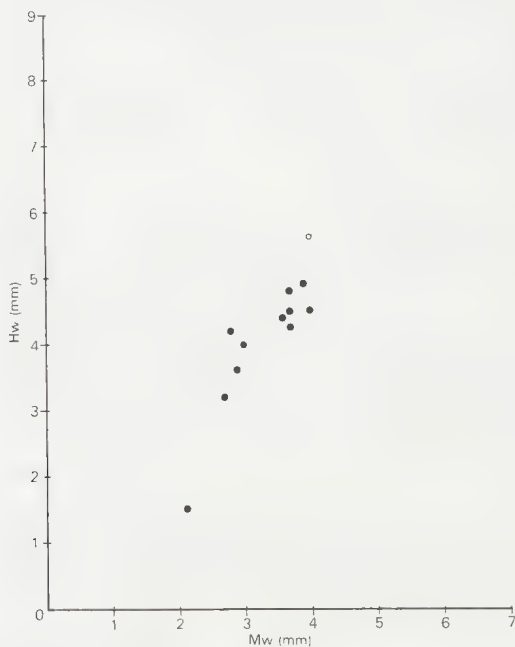


Figure 9. Scatter diagram of Hw:Ldv for *Notanoplia philipi* sp. nov.

posterior margin is linear. The ventral valve is moderately convex whilst the dorsal valve is planar to slightly concave.

The exterior of the shell is costate (pl. 6, fig 32, pl. 7, figs 2, 4-10) with the costae increasing anteriorly by intercalation. The costae originate from the umbones of the valves and the hingeline, and number 4 to 5 per mm measured at the anterior commissure.

Interior of the ventral valve: The hinge teeth are relatively large and formed without the development of ventral adminicula. They are widely divergent and project anteriorly beyond the hingeline. The delthyrium is open, triangular and wide. A narrow triangular ventral muscle field is situated in the posterior portion of the delthyrial cavity where it is flanked by the lateral septa. The lateral septa originate anterolaterally to the muscle field; they are smooth and diverge from each other at angles of 80° to 100°. A moderately deeply impressed median septum originates anterior to the ventral muscle field and bifurcates one-sixth to one-quarter of the distance to the anterior commissure. The two portions of the septum remain subparallel. The anterior rim of the valve is sculptured by grooves which probably reflect the position of setae in life.

Interior of the dorsal valve: The sockets are shallow and widely divergent. They are defined by short plate-like socket ridges originating from the apex of the notothyrium. The socket plates fuse posteriorly to form a scroll-like cardinal structure which is raised above the level of the floor of the valve and projects slightly beyond the hingeline, as illustrated by Philip (1962, pl. 31, fig. 14). A pair of divergent, smooth impressed lateral septa originate anterolaterally to the cardinalia at about the same distance as the median septum. The septum is deeply impressed and bifurcates almost immediately. The interior is sculptured with a mosaic of fine pits in MUGD 3440 (pl. 7, fig. 1) and they appear to represent the impressions of the individual shell fibres. The anterior rim of the valve is sculptured with fine grooves which correspond to the costae on the external surface; they may have borne the setae during

life. Some of the grooves are punctured by larger circular depressions than the cell mosaic, and are linearly arranged. I believe these depressions to represent the position of pseudopunctae in the shell. This is supported by Dr G. A. Thomas (1978, oral comm.).

Discussion: The absence of "crested" lateral septa in both valves supports the generic placement of this species in *Notanoplia* as originally proposed by Philip (1962) rather than *Boucotia* as suggested by Gill (1969).

N. philipi is distinguished from *N. pherista* by the well developed costae on the external surface of the shell. Savage (1974, p. 28) noted that *N. pherista* is smooth to very faintly costate.

The report of pits in setal grooves has not been described elsewhere in Notanopliidae. The closeness in form, linear spacing and position recalls the linearly arranged pits of the pseudopunctae of strophomenides particularly among the Chonetidina.

Occurrence: *N. philipi* sp. nov. is confined to the Melbourne Trough where it is known from four localities. Loc. 43 and 54/60 in the Boola Formation 4 km west of W. 3 and Tyers Rd Junction along W 3. It is also known from loc. 87 (Gill, 1969, p. 1227) from the Humevale Formation at Lilydale.

Range: Early Devonian (Late Lochkovian).

Genus *Boucotia* Gill, 1969

Type species: *Anoplia australis* Gill, 1942, p. 38-9 pl. IV, fig. 8.

Diagnosis: Notanopliids with crested septa in both dorsal and ventral valves or in the ventral valve only.

Discussion: See also under discussion of *Notanoplia*. *Boucotia* was erected by Gill (1969, p. 1227) on the basis that all species of *Boucotia* possess crested septa in both valves. In his diagnosis and description of the type species *B. australis* he failed to include a description of illustration of the holotype

MUGD 1720. Re-examination of the holotype, has revealed that the septa in the dorsal valve lack the crested septal condition. The ventral valve does have crested septa as described by Gill (1969, p. 1228) for the species. Furthermore all specimens that Gill assigned to *B. australis* from locality 87, likewise have smooth, uncrested septa in the dorsal valve. They conform to the morphology of the holotype; as Gill noted (1969, p. 1228) it "is difficult to demonstrate the crestal furrows on the crest septa". His illustrations (pl. 143, figs. 13-18) apparently show well developed crestal furrows (see particularly his pl. 143, figs. 14, 16 and 18). However, detailed examination of his dorsal valve latex cast and the specimen P25497 does not reveal any trace of crestal furrows on the septa. Specimen P25551 illustrated by Gill (1969, pl. 144, fig. 11) from locality 23, which is in the lower part of the Humevale Formation does have crested septa in both valves. This condition occurs in all specimens examined from the lower part of the Humevale formation at Lilydale. It is the ancestral condition of the genus. It is here described as *Boucotia janaea* sp. nov. Other species of *Boucotia*, *B. withersi* (Gill) and *B. loyolensis* (Gill) have crested septa in both valves.

Species assigned to Boucotia: B. australis, B.

withersi, B. janaea sp. nov. and *B. loyolensis*; all from the Lower Devonian of the Tasman Sub-province. *B. aff. australis* from the Guguro-Chumikansk Region of far eastern U.S.S.R. (Gratsianova and Schisckina, 1977, p. 2) belongs to *Boucotia*, but its specific affinities remain doubtful until dorsal valves of the species are described.

Species rejected from Boucotia: B. incognita Langenstrassen, 1972, from the Middle Devonian of Germany. This species belongs to *Plicanoplites* Havlicek, 1974.

Range: Early Devonian (Lochkovian to ? Zlichovian).

***Boucotia australis* (Gill, 1942)**
(Plate 7, figs. 11-16, 18-31)

Synonymy:

- 1940 *Anoplia* sp. nov.,—Gill, pp. 251, 255–6 (name only).
1941 *Anoplia* sp. nov.—Gill, p. 157 (name only).
1942 *Anoplia australis* Gill, p. 38-39, pl. IV, fig. 8.
1945a *Anoplia australis* Gill—Gill, p. 144.
1945b *Anoplia australis* Gill—Gill, p. 123 (name only).
1948 *Anoplia australis* Gill—Gill, p. 13 (name only).
1949 *Anoplia australis* Gill—Singleton, p. 251.
1950a *Anoplia australis* Gill, p. 85 (name only).
1950b *Anoplia yeringae* Gill (nom. nud.) p. 52 fig. 2c.
1951a *Anoplia australis* (Gill)—Gill p. 251 (name only).
1951b *Notanoplia australis* (Gill)—Gill p. 64.

Dimensions of some specimens of *Boucotia australis* (Gill)

Registered Number	Hw	Mw	Lvv	Ldv	(v) Lms	(v) <ls	(d) Lms	(d) <ls	setae per mm
MUGD 1720 (Holotype)	5.0	5.8	4.3	4.3	3.2	90°	2.4	90°	
NMV P25475	3.9	4.4	3.4		2.8	85°			
NMV P25483	5.3	5.3	4.7	4.7	?	?	4.1	?	4
NMV P25496	4.4	5.0		4.6			3.5	70°	5
NMV P25497	4.6	4.6		3.7			2.5	75°4	
NMV P25505	4.8	4.8	3.9		1.7	90°			
NMV P25506	3.4	3.7	3.3		2.8	65°			
NMV P25507	3.6	4.0	3.0	3.0	2.1	75°	?	90°	
NMV P25508	3.5	3.8	3.1		?				
NMV P25511	2.3	2.5	2.2		1.8	80°			
NMV P25526	3.4	3.4	2.8		2.2	80°			
NMV P25503	5.5	5.5	4.6		3.8	?			
NMV P25514	5.3	5.1	3.6	3.6	3.1	80°	3.2		

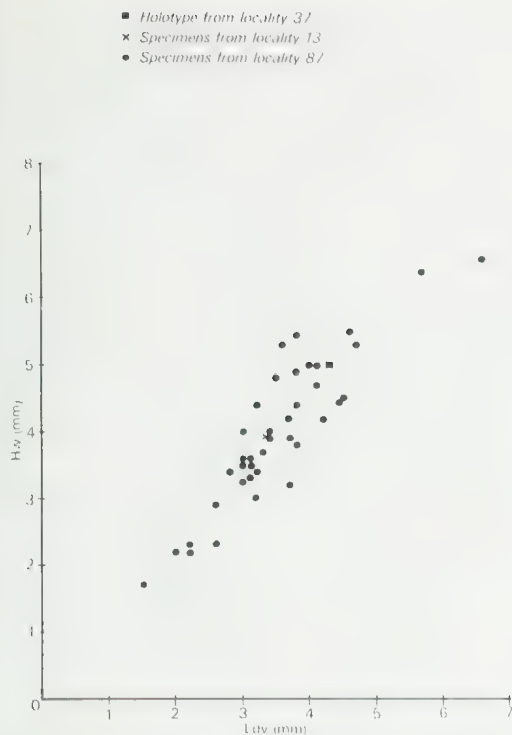


Figure 10. Scatter diagram of Hw:Lvv for *Boucotia australis* (Gill)

- 1960 *Notanoplia australis* (Gill)—Philip p. 147, 150 (name only).
 1962 *Notanoplia australis* (Gill)—Philip p. 206-7, pl. XXXI, figs. 9, 10, Fig. 13a.
 1965 *Notanoplia australis* (Gill)—Gill p. 120 (name only).
 1969 "*Notanoplia*" *australis* (Gill)—Boucot, Johnson, Talent, p. 89, pl. 10, figs. 7, 9.
 1969 *Boucotia australis* (Gill)—Gill, p. 1227-9, text figs. 3, 4, pl. 143, figs. 9-21, pl. 144, figs. 1-10, 13, 14.
 1972 *Boucotia australis* (Gill)—Strusz, p. 432-3 (name only).
 1974 *Boucotia australis* (Gill)—Savage, p. 29 (name only).
 ?1977 *Boucotia* aff. *australis* (Gill)—Gratsianova and Schischkina, p. 27, 28, pl. XXII, figs. 6, 7.

Diagnosis: *Boucotia* with crested septa in the ventral valve.

Holotype: MUGD 1720 which is an internal mould of an articulated specimen described by Gill (1942, p. 38, 39, pl. IV, fig. 8).

Figured specimens: NMVP 25475, NMVP 25497, NMVP 25503, NMVP 25505-8,

Figure 12. Scatter diagram of Hw:Ldv for *Boucotia australis* (Gill).

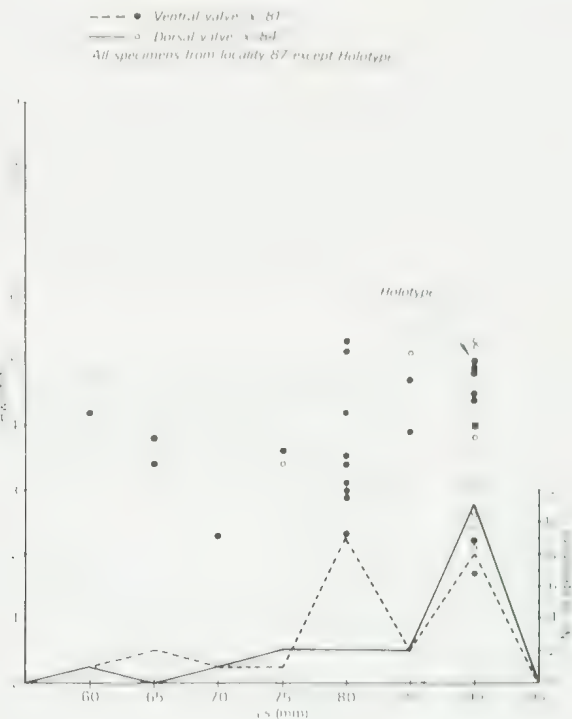
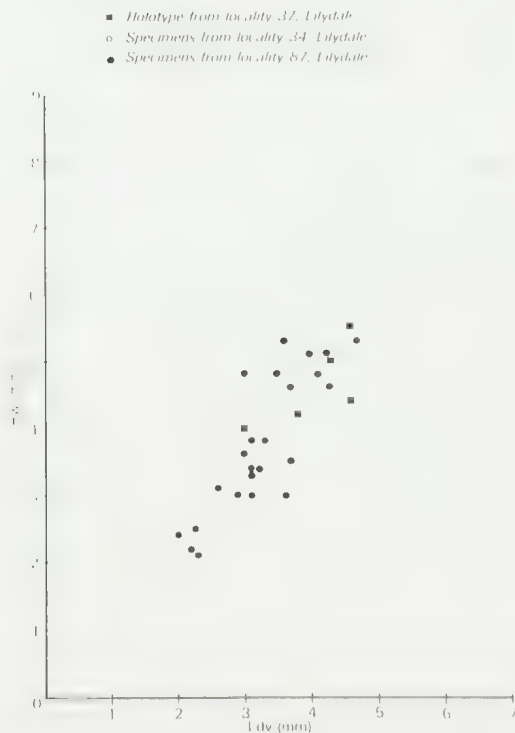


Figure 11. Diagram of Hw:Ls for *Boucotia australis* (Gill), frequency plotted as a curve.



NMVP 25514, NMVP 25501, NMVP 25483, NMVP 25496, MUGD 3439a & b, MUGD 3442.

Type locality: Seville Quarry on Warburton Highway, approx. 2 km east of Seville. Coords. Ringwood 1:63360, 497413; it is locality 37 of Gill (1945a, p. 184).

Type strata: Humevale Formation.

Material: Description is based on 33 ventral and 23 dorsal valves and 6 internal moulds of conjoined valves from loc. 87 (Gill, 1969), 1 ventral valve from loc. 13 (Gill, 1942) and 1 internal mould of articulated specimen from loc. 37.

Description: The holotype MUGD 1720 which is an articulated specimen from locality 37, Seville Quarry, Seville, Victoria has not been adequately described or illustrated. This is rectified and comparisons are made with collections from other localities where variation in morphology are apparent.

Despite a detailed search at the type locality and in collections stored at the National Museum of Victoria and the Melbourne University Geology Department, no topotype material has been found.

Exterior: The shells are small, with a variable outline ranging from shield shaped to quadrate. The width exceeds the length of the shell. They are concavo-convex to plano-convex in lateral profile. The hingeline is straight with a maximum width usually anterior to the hingeline, but in NMV P25512, P25526 (pl. 7, fig. 31) and P25454 for example the maximum width is at the hingeline. A low apsacline ventral interarea occurs on either side of the delthyrium and terminates about half the distance to the cardinal extremities of the valve. The ventral valve is moderately convex whilst the dorsal valve is planar to slightly concave.

The surface of the shell is usually smooth but in NMV P25547 and P25548 concentric growth lines are located near the anterior commissure.

Interior of the ventral valve: The hinge teeth are relatively large lacking ventral adminicula. The

delthyrium is open, triangular and wide. A narrow pedicle tube (Gill, 1969, p. 1227) lies on the floor of the delthyrial cavity, posterior to the median septum. It is well preserved in NMV P25475 and NMV P25506 (pl. 7 figs. 15, 24, 25). The lateral septa originate anterolaterally to the muscle field and diverge from each other at an angle of 60° to 90° (mean 81° (Fig. 11) in specimens from loc. 87). The lateral septa are narrow but in the holotype MUGD 1720, they broaden out towards the lateral edges of the valve. The crests of the lateral septa are grooved. A low narrow median septum arises anterior to the pedicle tube and terminates abruptly approximately 1 mm from the anterior commissure. In the holotype MUGD 1720 it is broad low and triangular in shape. It occasionally bifurcates as in NMV P25507 (pl. 7, figs. 26, 27). In NMV P25505 (pl. 7, fig. 23) the septum originates in mid length. The crestal furrows give a beaded appearance to the septum, in internal moulds.

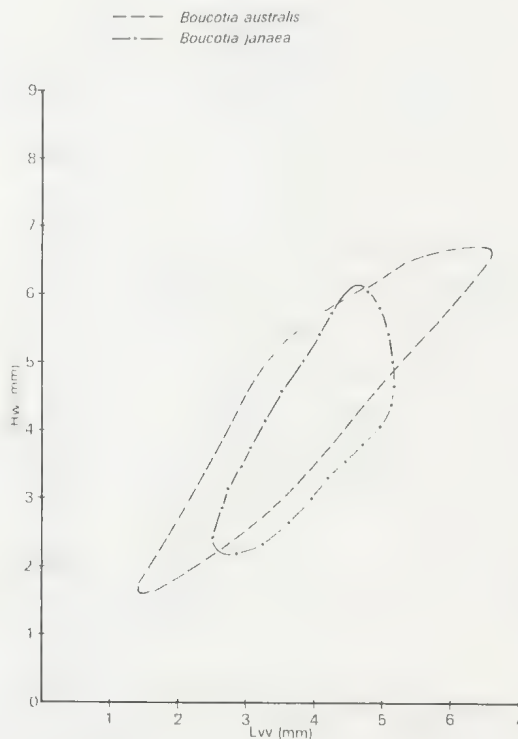


Figure 13. Envelopes surrounding points in graphs of Hw:Lvv in Figures 10 & 14.

Interior of the dorsal valve: The sockets are widely divergent. They are defined by short plate-like socket ridges originating laterally to the scroll-like cardinal process. The cardinal process is raised above the floor of the valve and recurves posteriorly to project beyond the hingeline (pl. 7, fig. 20). The lateral septa are smooth and linear but in NMV P25495 and NMV P25497 they are slightly curved and project anteriorly (pl. 7, fig. 20). Divergence of the lateral septa from the cardinalia is between 60° and 90° (mean 84° in specimens from loc. 87). Dorsal median septum is narrow, linear arises anterior to the cardinalia and terminates abruptly between 1 mm and .5 mm from the anterior commissure. The anterior margin is sculptured by fine grooves 4 to 5 per mm which are probably setal grooves. These were termed capillae by Gill (1969, p. 1228). Otherwise the surface is smooth.

Discussion: The absence of septa (i.e. smooth septa) in the dorsal valve of *Boucotia australis* distinguishes it from *B. janaea* sp. nov. which has pitted crested septa in the dorsal valve. *B. withersi* and *B. loyolensis* are distinguished from *B. janaea* by having 5 and 7 crested septa respectively in the dorsal and ventral valves. Gill (1951a, p. 64) stated that "there is a smaller variety of this species (his concept of *B. australis*) present at Ruddock's Quarry and many other Lower Yeringian localities, while in the Upper Yeringian this species is represented by a larger variety". This claim has not been verified in the present study. Scatter diagrams of *B. australis* and *B. janaea* show similar size ranges of populations separated by thousands of feet of strata (see Fig. 13). Gill (op. cit.) also stated that "there are small differences in structure". An assessment of the angle between the lateral septa of *B. australis* and *B. janaea* both show that the angle between the lateral septa of the dorsal valve is larger than that of the ventral valve. Mean for angle in ventral valve 80.4° and 81° , and dorsal valve, 86.4° and 84° for *B. janaea* and *B. australis* respectively. These differences are not considered significant.

The persistent difference in the angles of the lateral septa of the ventral and dorsal valve of both species allows the septa to overlap as il-

lustrated by Gill (1969, text fig. 4, p. 1228), with one significant modification, the lateral septa of the ventral valve lie *inside* those of the dorsal valve. His drawing of P25483 has the dorsal and ventral valves reversed!

The lateral and median septa of the shell are thought to have functioned as lophophore supports in a similar manner to those of the Chonetacea as postulated by Grant (1976, p. 65, text fig. 11) for *Chonetina*.

Occurrence: *B. australis* is known from Gill's loc. 1, 3, 13, and 87 of the Lilydale district. It is known from Kinglake (w5) and Heathcote districts (loc. 54, Parish of Redcastle Talent, 1965).

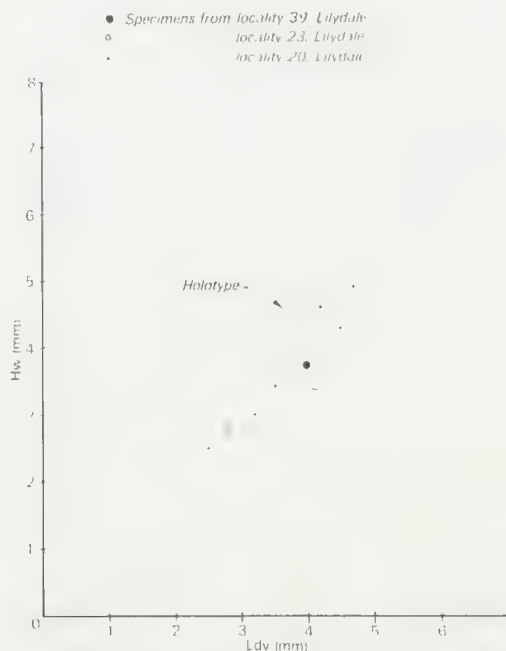
Range: Early Devonian (Late Lochkovian to Early Praguian).

***Boucotia janaea* sp. nov.**

(Plate 7, fig. 32, Plate 8, figs. 1-7, 9-25)

Synonymy: 1969 *Boucotia australis* (Gill)—Gill, pl. 144, fig. 10.

Diagnosis: *Boucotia* with three crested septa in both valves.



Dimensions of some specimens of *Boucotia janaea* sp. nov.

Registered Number	Hw	Mw	Lvv	Ldv	(v) Lms	(d) Lms	(v) <ls	(d) <ls	Setae per mm
NMVP 25471	4.9	6.1		4.7					3
NMVP 49728	3.4	4.1		3.5		2.3	90°		
NMVP 49729	3.0	4.6		3.2		2.5	90°		
NMVP 49730	3.8	4.8	4.5		2.9		80°		
NMVP 49731	5.0	5.4	5.0		4.0		80°		
NMVP 25465	3.4	4.2	4.1	4.1	3.3	3.3	80°	90°	
NMVP 25478	4.6	4.6	4.0	4.0	3.0	3.0	70°	85°	

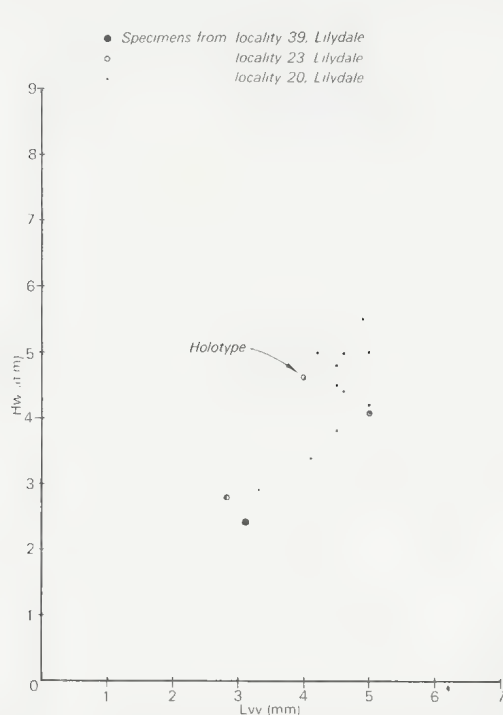


Figure 15. Scatter diagram of Hw:Ldv for *Boucotia janaea* sp. nov.

Derivation of name: After Jan, whose help and support in this paper is gratefully acknowledged.

Holotype: NMV P25478, which is an internal mould of an articulated specimen, figured herein, pl. 8, figs. 3-5.

Paratypes: NMV P25465, NMV P25551.

Figured Specimens: NMV P25471, NMV P49730, NMV P49731.

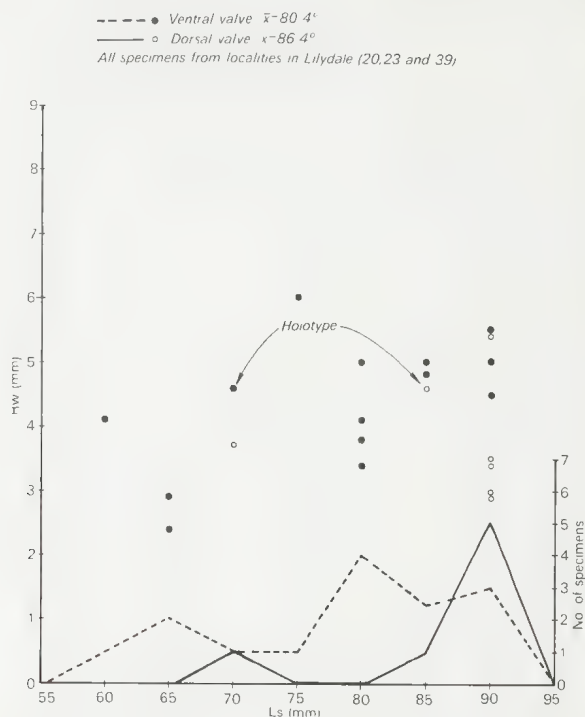


Figure 16. Diagram of Hw:Ls for *Boucotia janaea* p. nov. with frequency plotted as curve. All specimens are from locs. 20, 23 and 39, Lilydale Victoria.

Type locality: Loc. 23, north of Ruddock's Quarry, Lilydale (Gill, 1940, p. 260).

Type strata: Humevale Formation.

Material: Description based on a total of 26 specimens of which two articulated specimens, two dorsal and 3 ventral valves are known from the type locality.

Description: The outline, range in size and shape replicates that of *B. australis* (text figs. 13, 14, 15).

Exterior: Shells are smooth.

Interior of ventral valve: Similar to the interiors of the ventral valve of *B. australis*.

Interior of dorsal valve: Lateral and median septa are smooth and show no pitting as in *B. australis*. Grooves interpreted as setal grooves are preserved near the anterior margin of the valve in two specimens from 2 to 3 per mm. Otherwise the interiors are similar to *B. australis*.

Discussion: See under *B. australis*.

Occurrence: Uncommon representative of the benthos in the lower part of the Humevale Formation at Gill's localities 20, 23, 3. Rare at localities P120, P98 and A4 north west of Whittelee (Williams, 1964).

Range: Early Devonian (Lochkovian).

***Boucotia loyolensis* (Gill, 1951b)**
(Plate 8, figs. 34-41)

Synonymy:

- 1913 *Leptaena rhomboidalis*, (Wilkins)—Chapman, p. 103-4, pl. X, figs. 6, 7.
1951b *Notanoplia loyolensis* Gill, p. 63-64, pl. 3, figs. 1-4.
1962 *Notanoplia loyolensis* Gill—Muir-Wood, pl. 5, figs. 8a, 8b.
1965 *Notanoplia loyolensis* Gill—Couper, p. 7.
1965 *Notanoplia loyolensis* Gill—Muir-Wood, p. 11426, Fig. 284.
1969 *Boucotia loyolensis* (Gill)—Gill, p. 1230, pl. 155, figs. 19-21.
1972 *Boucotia loyolensis* (Gill)—Strusz, p. 441 (name only).
1974 *Boucotia loyolensis* (Gill)—Savage, p. 29 (name only).

Holotype: NMV P12403 which is an internal mould of the ventral valve, originally illustrated by Chapman (1913, pl. X, Figs. 6, 7) and later by Gill (1951, pl. 111, figs. 1-4) and Muir-Wood, 1965, p. H426, Fig. 284, 3b, c; it was discovered by Mr. George Sweet.

Figured specimens: NMV P25542, NMV P28003, NMV P28035, NMV P49720, NMV P49740-2.

Type locality: Near Loyola, Quarry south west of Mansfield.

Type strata: Norton Gully Sandstone.

Material: A rare species at every locality where it has been found. Description is based on a total of 5 internal moulds of the ventral valve and 3 internal moulds of the dorsal valve. Dimensions of figured specimens of *Boucotia loyolensis* are shown overleaf.

Description: A full description of *B. loyolensis* is given because until now the interior of the dorsal valve was unknown.

Exterior: Shells average size for the genus, subquadrate in outline with a straight hingeline. The maximum width is usually anterior to the hingeline at about mid-length of the shell. A low apsacline ventral interarea flanks the open delthyrium extending two-thirds of the distance to the cardinal extremities of the shell. The ventral valve is convex whilst the dorsal is slightly concave. Exterior of the shell unknown.

Dimensions of figured specimens of *Boucotia loyolensis*

Registered Number	Hw	Mw	Lvv	Ldv	(v) Lms	(d) Lms	(v) <as ₁	(v) <ls	(v) <as ₂	(d) <as ₁	(d) <ls	(d) <as ₂	Costae per mm	Hd	Wd
NMV 25542	2.5	2.5		2.5									3		
NMV 49720	3.0	3.0		2.3		2.3				20°	75°	120°			
NMV 12403	6.8	7.2	5.7		3.8		40°	90°	140°					1.2	1.7
NMV 28003	6.0	6.6	5.8		5.6		30°	90°	130°						
NMV 28035	4.7	5.2	4.2		3.8		30°	90°	140°						
NMV 49740	4.7	5.7	4.6		3.7		30°	90°	130°						
NMV 49741	4.0	5.0		3.8		3.2				35°	95°	150°			
NMV 49742	5.6	6.0	5.5		4.4		45°	90°	130°						

Interior of the ventral valve: The hinge teeth project anteriorly beyond the hingeline in holotype NMV P12403, are divergent and formed without any development of ventral ad-minicula. In NMV P28003 (pl. 8, fig. 34) a narrow ventral muscle field is situated posterior to the median septum and flanked by the second pair of lateral septa. Three pairs of lateral septa are present, the inner and outermost pairs originating mid way to the anterior commissure whilst the middle pair originate close to the ventral umbo. In NMV P28003 the outer pair are smooth, pits only being developed on the middle, inner pairs of lateral septa and the median septum. In the holotype only the inner pair of laterals are smooth. The inner pair of lateral septa diverge at an angle of 30° to 45°, middle pair at 90°, and the outer pair between 130° and 140°. All three pairs of lateral septa and the median septum broaden anteriorly.

Interior of the dorsal valve: The sockets are shallow and widely divergent. The cardinal process is not preserved. The arrangement, development and form of the lateral septa replicates those of the ventral valve. Angle of divergence of the inner pair of lateral septa is between 20° and 35°, middle pair 75° to 95° and the outer pair 120° to 150°. The outer pair are smooth, whilst the inner and middle pairs of lateral septa are pitted.

Occurrence: Most of the specimens of *B. loyolensis* have been found in the Eildon district in the Norton Gully Sandstone, at Loloya Quarry near Mansfield, Jerusalem Creek, near Eildon, and 12 chains southwest of low saddle at the head of the right branch of Cales Creek, a tributary of the Big River near Enoch's Pt. Two other occurrences should be noted, locality 10 of Harris and Thomas (1942) at Yea in the Flowerdale Conglomerate Member (Couper, 1965) and locality 87, Lilydale in the upper beds of the Humevale Formation (Gill, 1969) (pl. 8, fig. 36).

Range: Early Devonian (Late Lochkovian to Praguian).

***Boucotia withersi* (Gill, 1942)** (Plate 8, figs. 26-33)

Synonymy:

- 1942 *Anoplia withersi* Gill—Gill, p. 39, pl. IV, fig. 7.
- 1945a *Anoplia withersi* Gill, p. 144-5.
- 1947 *Anoplia withersi* Gill—Gill, p. 13 (name only).
- 1949 *Anoplia withersi* Gill—Singleton, p. 251 (name only).
- 1950a *Anoplia withersi* Gill—Gill, p. 85 (name only).
- 1950b *Anoplia withersi* Gill—Gill, p. 52, 53 (name only).
- 1951 *Notanoplia withersi* (Gill)—Gill, p. 251 (name only).
- 1960 *Notanoplia withersi* (Gill)—Philip, p. 150 (name only).
- 1964 *Notanoplia withersi* (Gill)—Williams, p. 282 (name only).
- 1969 "*Notanoplia*" c.f. *withersi* (Gill)—Boucot, Johnson & Talent, p. 89, pl. 10, fig. 8.
- 1969 *Boucotia withersi* (Gill)—Gill, p. 1229, pl. 143, Figs. 21, pl. 144, figs. 1, 12, 15-18.
- 1972 *Boucotia withersi* (Gill)—Strusz, p. 432 (name only).
- 1974 *Boucotia withersi* (Gill)—Savage, p. 29 (name only).

Holotype: MUGD 1721, which is an internal mould of the ventral valve and described by Gill (1942, p. 39, pl. IV, fig. 7).

Figured specimens: NMV P25446, NMV P25447, NMV P25456, NMV P25458, NMV P25459.

Type locality: Symes Tunnel, Killara; loc. 34 of Gill (1945a, p. 184).

Type strata: Humevale Formation.

Diagnosis: *Boucotia* with two pairs of lateral septa in each valve.

Material: 3 internal moulds of the ventral valve and one internal and external mould of the dorsal valve.

Description: Exterior: Only dorsal exterior is known, which bears faint costae. The outline, convexity of valves and size correspond to *B. janaea* sp. nov.

Interior of the ventral valve: The open delthyrium, teeth and pedicle tube of *B. withersi*, are identical to those of *B. australis*. The

Dimensions of figured specimens of *B. withersi*

Registered Number	Hw	Mw	Lvv	Ldv	(v) Lms	(d) Lms	(v) <as _i	(v) <ls	(d) <as _i	(d) <ls
MUGD 1721	3.8	4.7		4.0						
NMV P25446	4.5	4.8		4.1		2.6			30°	90°
NMV P25447	4.2	4.4	3.9		3.3		75°	75°		
NMV P25456	5.4	7.0	5.6		5.0		90°	90°		
NMV P25458	4.6	5.3	4.2		4.0		40°	90°		
NMV P25459	5.3	6.5	6.5		3.6		30°	90°		

muscle field is not preserved. The lateral septa are crested and diverge at an angle 75° to 90°. They are usually narrow but in NMV 25459 they are deeply incised and broader anteriorly. The median septum originates anterior to the pedicle tube and terminates abruptly close to the anterior commissure. The accessory lateral septa originate between the lateral and median septa in two ways, as described by Gill (1969, p. 1229). They either (1) originate close to the lateral septa in the posterior portion of the valve as in NMV 25459 (pl. 8, fig. 33) diverging at an angle of 30° to 40°, or (2) arise from the median septum at its mid length diverging parallel to the lateral septa as in NMV 25456 (pl. 8, fig. 31) NMV 25447 (pl. 4, figs. 29, 30). The accessory septa are smooth.

Interior of the dorsal valve: Socket ridges and cardinal process are similar to those of *B. australis*. The lateral septa are thin, linear and crested, diverging from the cardinalia at 90°. Accessory septa are thin, linear and originate between the lateral and median septa in mid length of the valve and curve slightly anteriorly. The median septum is crested and terminates abruptly 1 mm from the anterior commissure.

Discussion: The holotype MUGD 1721 was originally described by Gill (1942, p. 39, pl. 4, fig. 7) as an internal mould of the ventral valve. This has since been destroyed leaving the external mould of the dorsal valve. Gill's description leaves no doubt that the specimen is *B. withersi*.

Gill (1969, p. 1229) noted that taxonomic significance of the variable development of the accessory septa could not be clarified because of lack of material. This still stands, *B. withersi* is a rare species at each of the localities where it occurs.

Occurrence: *B. withersi* occurs at loc. 33, 34, 41 and 87 at Lilydale (Gill, 1969, p. 1229) and Tommy's Hut, Kinglake. All specimens referred to *B. withersi* by Gill (1969, p. 1229) from loc. 20, 21, 26 and 39 Lilydale, and west of Yankee Jim Creek, undoubtedly belong to *B. janaea* sp. nov.

Range: Early Devonian (Late Lochkovian to Early Praguian).

Acknowledgements

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Explanation of Plates

PLATE 5

Notoparmella plentiensis sp. nov.

All figures $\times 5$ and from loc. A 17, Plenty, Victoria.

- Figs. 1. NMV P49695a Holotype, internal mould of articulated specimen.
2. NMV P49695b Holotype, external mould of same.
3. NMV P49601 Paratype, internal mould of ventral valve, note development of muscle scars.
4. NMV P49603 Paratype, internal mould of dorsal valve.
5. NMV P49607 Paratype, external mould of ventral valve, note fine costellae.
6. NMV P49604 Paratype, internal mould of ventral valve.
7. NMV P49610 Paratype, internal mould of ventral valve.
8. NMV P49614 Paratype, external mould of dorsal valve.
9. NMV P49613 Paratype, internal mould of ventral valve.
10. NMV P49608 Paratype, external cast of ventral valve, note the bifurcation of the median septum.
11. NMV P49616a Paratype, external mould of dorsal valve.
12. NMV P49616b Paratype, internal mould of dorsal valve, a wide form.
13. NMV P49625 Paratype, internal mould of ventral valve.
14. NMV P49628 Paratype, internal mould of ventral valve.
15. NMV P49637 Paratype, internal mould of dorsal valve.
16. NMV P49641 Paratype, internal mould of ventral valve.
17. NMV P49642 Paratype, internal mould of ventral valve.
18. NMV P49644 Paratype, internal mould of dorsal valve.
19. NMV P49647 Paratype, internal mould of ventral valve.
20. NMV P49652 Paratype, external mould of dorsal valve.
21. NMV P49666 Paratype, internal mould of dorsal valve.
22. NMV P49664 Paratype, internal mould of ventral valve, a narrow form.
23. NMV P49674 Paratype, internal mould of ventral valve.

24. NMV P49697a Paratype, internal mould of dorsal valve.
25. NMV P49697b Paratype, external mould of dorsal valve.
26. NMV P49699a Paratype, internal mould of dorsal valve, note form of cardinal process.
27. NMV P49699b Paratype, external mould of dorsal valve.

PLATE 6

All figures $\times 4$

- Figs. 1-3 *Notoparmella plentiensis* sp. nov., from Sugarloaf Dam Christmas Hills, Victoria.
1. NMV P49750a internal mould of ventral valve.
2. NMV P49750b external mould of ventral valve.
3. NMV P49751 internal mould of ventral valve.
- Figs. 4-18 *Notanoplia pherista* Gill.
- 4-15 from loc. 16, Zeehan Tasmania.
- 16-18 from loc. W5, Kinglake, Victoria.
4. NMV P14827 Holotype, latex cast of ventral valve, note smooth lateral septa.
5. NMV P14827 Holotype, internal mould of ventral valve.
6. NMV P14790 Hypotype, external mould of dorsal valve, note very fine costellae.
7. NMV P14827a Paratype, internal mould of dorsal valve.
8. NMV P14827b Paratype, internal mould of dorsal valve.
9. NMV P25557 Hypotype, internal mould of ventral valve.
10. NMV P25559 Hypotype, internal mould of ventral valve, note development of pedicle tube.
11. NMV P25561 Hypotype, internal mould of ventral valve.
12. NMV P25561 Latex cast of ventral valve.
13. NMV P25562 Hypotype, internal mould of ventral valve.
14. NMV P25563 Hypotype, internal mould of ventral valve.
15. NMV P25564 Hypotype, external mould of dorsal valve, note concentric lamellae and incipient costellae.
16. NMV P49721 internal mould of ventral valve, note incipient lateral and median septa.
17. NMV P49722a internal mould of ventral valve.
18. NMV P49722b external mould of ventral valve.
- Figs. 19-26 *Notanoplia panifica* sp. nov., from Sugarloaf Dam Christmas Hills, Victoria.
19. NMV P49746 Holotype, internal mould of ventral valve, note incipient development of lateral septa.
20. NMV P49745 Paratype, internal mould of ventral valve.
21. NMV P49747a Paratype, external mould of dorsal valve, note development of fine incipient costellae.
22. NMV P49747b Paratype, internal mould of dorsal valve, note incipient lateral septa.
23. NMV P49748a Paratype, internal mould of dorsal valve, note incipient accessory septum.

24. NMV P49748b Paratype, external mould of dorsal valve.
 25. NMV P49753 Paratype, internal mould of ventral valve, note well developed pedicle tube.
 26. NMV P49754 Paratype, external mould of dorsal valve.
 Figs. 27-32 *Notanoplia philipi* sp. nov.
 27-30 from loc. 43, Parish of Boola, Tyers, Victoria.
 31-32 from loc. 54/60 Parish of Boola, Tyers, Victoria.
 27. MUGD 3441a Holotype, internal mould of ventral valve, note development of costae anteriorly.
 28. MUGD 3441b Paratype, internal mould of ventral valve.
 29. MUGD 3443 Paratype, internal mould of dorsal valve.
 30. MUGD 3444 Paratype, internal mould of ventral valve.
 31. NMVP 49718a, internal mould of ventral valve.
 32. NMVP 49781b, external mould of ventral valve.

PLATE 7

Figure 1 \times 14; Figures 2-33 \times 4

- Figs. 1-10 *Notanoplia philipi* sp. nov.
 1. From loc. 36, Parish of Boola, Tyers, Victoria.
 2-10 from loc. 87, Lilydale, Victoria.
 1. MUGD 3440 internal mould of dorsal valve, note small cardinal process, large pits in the lateral septa and grooves between costae, and ovate muscle scars.
 2. NMV P49720, external mould of dorsal valve.
 3. NMV P25487 internal mould of ventral valve.
 4. NMV P25488 external mould of dorsal valve, note costae.
 5. NMV P25489, external mould of dorsal valve.
 6. NMV P25494, external mould of dorsal valve.
 7. NMV P25542, external mould of dorsal valve.
 8. NMV P25535, external mould of dorsal valve.
 9. NMV P49723 external mould of articulated specimen.
 10. NMV P49724 external mould of dorsal valve.
 Figs. 11-16 *Boucotia australis* (Gill)
 11. MUGD 3442 internal mould of ventral valve from loc. 43, Parish of Boola, Tyers, Victoria.
 12. MUGD 3439a, internal mould of ventral valve from loc. 47, Parish of Boola, Tyers, Victoria.
 13. MUGD 1720 Holotype, internal mould of articulated specimen, note pitted crest septa in ventral valve only, from loc. 33, Seville, Victoria.
 14. MUGD 3439b, internal mould of ventral valve from loc. 47, Parish of Boola, Tyers, Victoria.

15. NMV P25475 internal mould of ventral valve, from loc. 13, Hull Road, Mooroolbark, Victoria.
 16. NMV P25483 internal mould of dorsal valve from loc. 87, Lilydale, Victoria.
 17. *Notanoplia philipi* sp. nov., NMV 25493 internal mould of dorsal valve, from loc. 87, Lilydale, Victoria.
 Figs. 18-31 *Boucotia australis* (Gill) from loc. 87, Lilydale, Victoria.
 18. NMV P25496 internal mould of dorsal valve.
 19. NMV P25497 internal mould of dorsal valve.
 20. NMV P25497 latex cast of dorsal valve, note smooth septa.
 21. NMV P25501 internal mould of articulated specimen.
 22. NMV P25503 internal mould of ventral valve.
 23. NMV P25505 internal mould of ventral valve.
 24. NMV P25506 internal mould of ventral valve.
 25. NMV P25506 latex cast of ventral valve, note pitted septa and pedicle tube.
 26. NMV P25507 internal mould of articulated specimen.
 27. NMV P25507 latex cast of articulated specimen.
 28. NMV P25508 latex cast of ventral valve, note smooth exterior.
 29. NMV P25514 posterior view of internal mould of articulated specimen.
 30. NMV P25514 ventral view, note pitted septa on ventral valve only.
 31. NMV P25526 internal mould of ventral valve.
 Fig. 32 *Boucotia janaea* sp. nov., NMVP 33089 Paratype external mould of ventral valve from loc. 23, Lilydale, Victoria.
 Fig. 33 *Notanoplia philipi* sp. nov., NMV P25539 external mould of dorsal valve from loc. 87, Lilydale, Victoria.

PLATE 8

All figures \times 4

- Figs. 1-7 *Boucotia janaea* sp. nov.
 1-5 from loc. 23, Lilydale, Victoria.
 6-7 from loc. 39, Lilydale, Victoria.
 1. NMV P25551 Paratype, internal mould of dorsal valve.
 2. NMV P25551 Paratype, latex cast of dorsal valve, note pitted crest septa.
 3. NMV P25478 Holotype, internal mould of articulated specimen.
 4. NMV P25478 Holotype, ventral view.
 5. NMV P25478 Holotype, dorsal view, note smooth septa.
 6. NMV P25444 internal mould of dorsal valve.
 7. NMV P25444 latex cast of dorsal valve, note pitted septa.
 Fig. 8 *Boucotia australis* (Gill) NMV 25445 external mould of dorsal valve, note concentric lamellae, from loc. 87, Lilydale, Victoria.

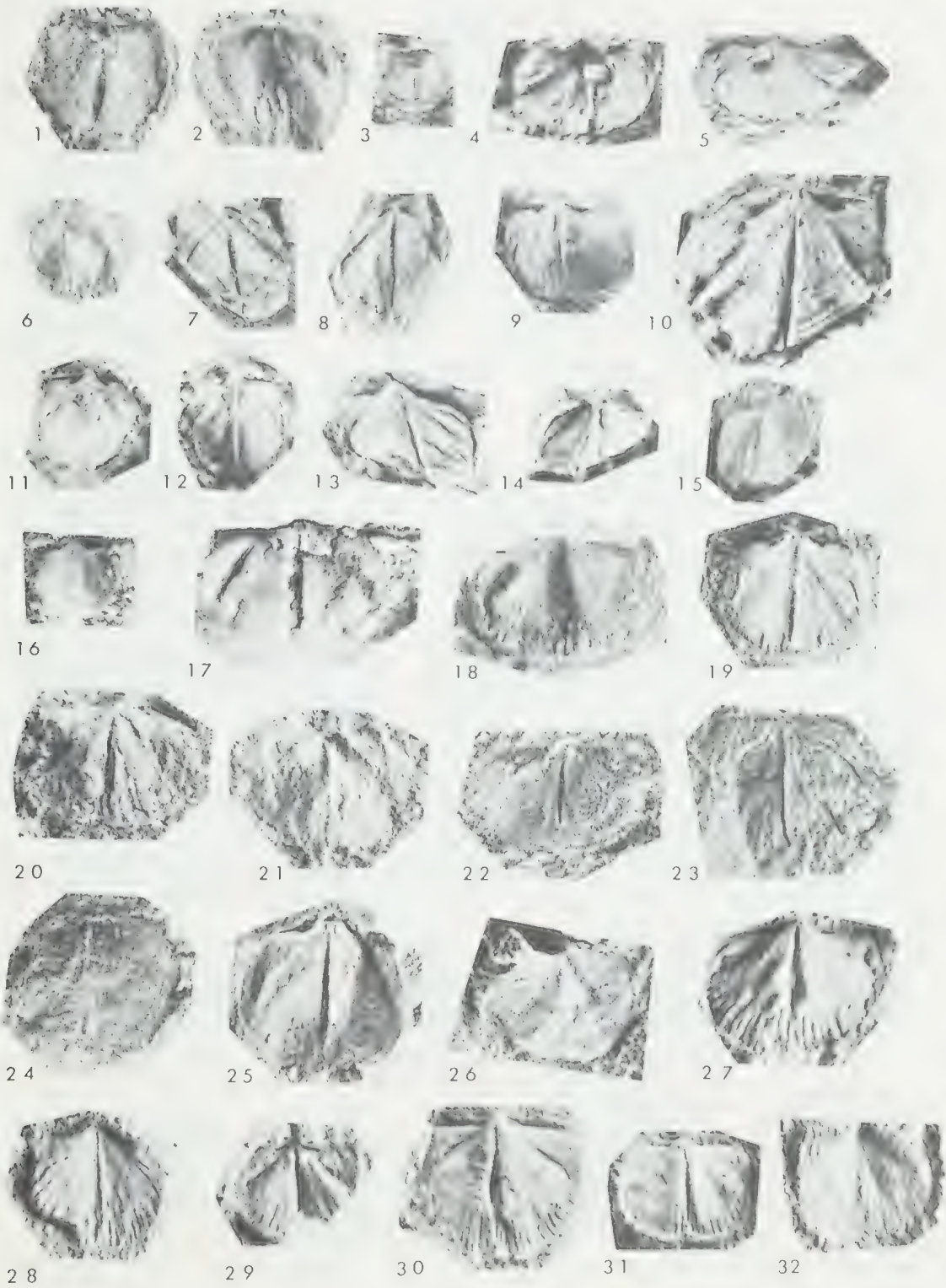
Figs. 9-25 *Boucotia janaea* sp. nov.

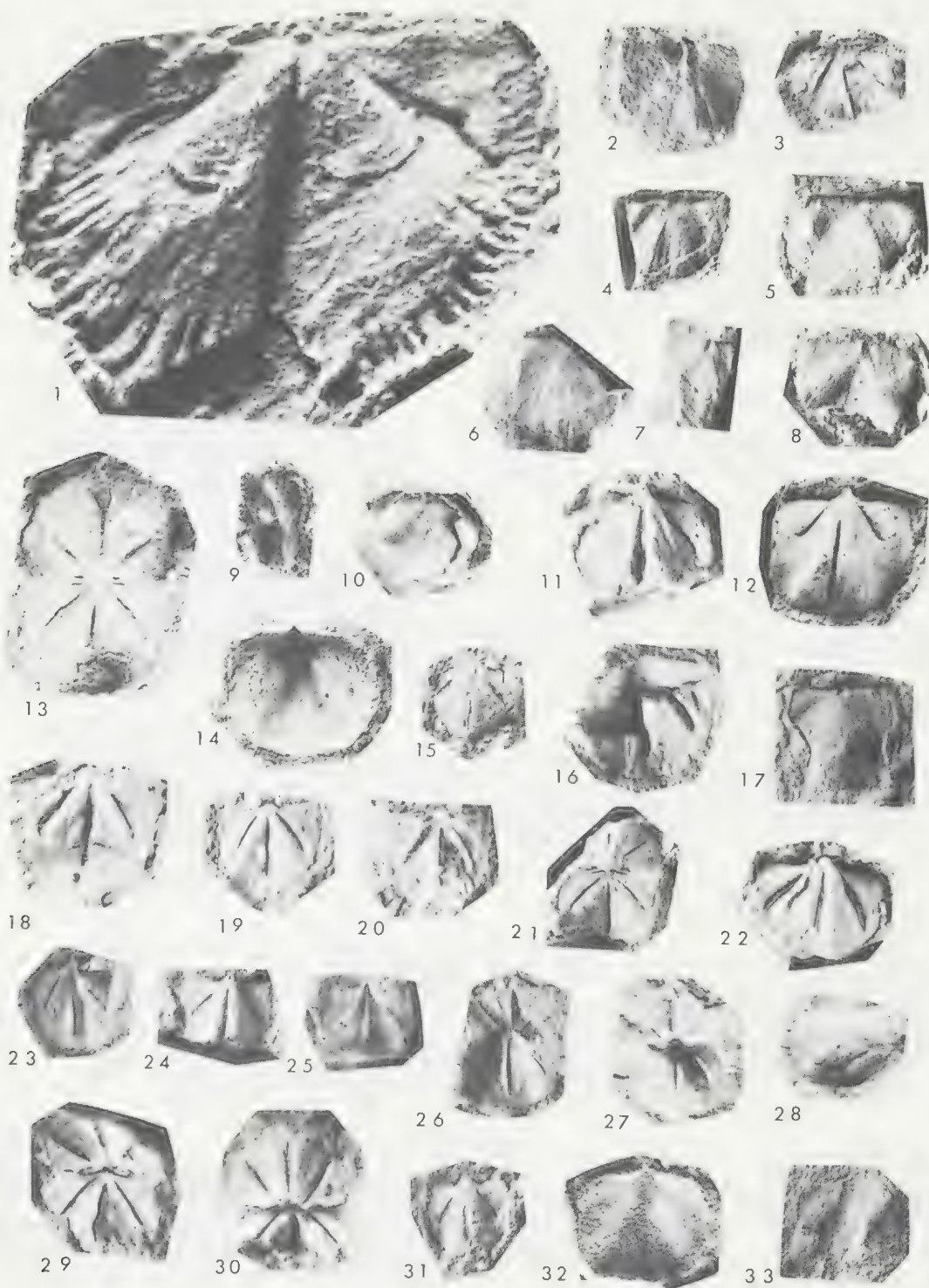
- 9-14, 16, 17 from loc. 20 Lilydale, Victoria.
 9. NMV P25463 internal mould of ventral valve.
 10. NMV P25464a, internal mould of ventral valve, note pedicle tube.
 11. NMV P49725 internal mould of ventral valve, note ovate muscle scars.
 12. NMV P25465 internal mould of articulated specimen.
 13. NMV P25466 internal mould of ventral valve.
 14. NMV P25467 internal mould of ventral valve.
 15. NMV P25468 Paratype, internal mould of ventral valve, from loc. 23, Lilydale, Victoria.
 16. NMV P25469 external mould of dorsal valve.
 17. NMV P25470 internal mould of ventral valve.
 18. NMV P25474 internal mould of ventral valve from loc. 39, Lilydale, Victoria.
 19. NMV P25471 external mould of dorsal valve from loc. 20, Lilydale, Victoria.
 20. NMV P25477 Paratype, external mould of dorsal valve from loc. 23, Lilydale, Victoria.
 Figs. 21-25 from loc. 20, Lilydale, Victoria.
 21. NMV P25480 external mould of dorsal valve.
 22. NMV P49728 internal mould of dorsal valve.
 23. NMV P49729 internal mould of dorsal valve.
 24. NMV P49730 internal mould of ventral valve.
 25. NMV P49731 internal mould of ventral valve.

Figs. 26-33 *Boucotia withersi* (Gill)

26. MUGD 1721 Holotype external mould of dorsal valve from loc. 34, Killara, Victoria.
 27. NMV P25446, internal mould of dorsal valve, note attitude of accessory septa, from loc. 87, Lilydale, Victoria.
 28. NMV P25446 latex cast of dorsal valve.
 29. NMV P25447 internal mould of ventral valve, from loc. 87, Lilydale, Victoria.
 30. NMV P25477 latex cast of ventral valve.
 31. NMV P25456 internal mould of ventral valve from loc. 87, Lilydale, Victoria.
 32. NMV P25458 internal mould of ventral valve from loc. 33, Killara, Victoria.
 33. NMV P25459 internal mould of ventral valve from loc. 33, Killara, Victoria.
 Figs. 34-41 *Boucotia loyolensis* (Gill)
 34. NMV 28003 internal mould of ventral valve, note small muscle scan near umbo, from 1 ml SE of junction of Jerusalem Creek and Barnwell Creek, Eildon, Victoria.
 35. NMV 28035 internal mould of ventral valve, from 12 chains SW of low saddle at head of right branch of Cables Creek Eildon, Victoria.
 36. NMV 49720 internal mould of dorsal valve, from loc. 87, Lilydale, Victoria.
 37. NMV 12403 Holotype, internal mould of ventral valve, from Loyola Quarry, Loyola, Victoria.
 38. NMV 12403 Holotype, latex cast of ventral valve.
 39. NMV 49740 internal mould of ventral valve, from Big River, Eildon, Victoria.
 40. NMV 49741 internal mould of dorsal valve, from Enochs Point near Eildon, Victoria.
 41. NMV 49742 internal mould of ventral valve from Enochs Point near Eildon, Victoria.









STUDIES ON AUSTRALIAN CAINOZOIC BRACHIOPODS 5.
THE GENERA *VICTORITHYRIS* ALLAN AND *DIEDROTHYRIS* NOV.

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Abstract

The genus *Victorithyris* is redefined and the species *V. peterboroughensis*, *V. garibaldiana*, *V. divaricata* and *V. tateana* redescribed. A new genus, *Diedrothyris*, is erected to include *Magellania johnstoniana* and *M. furcata* which are redescribed and a new species *D. plicata*.

Introduction

Victorithyris and *Diedrothyris* contain species occurring in Australian Tertiary deposits. They include all the Australian Tertiary species attributed previously to *Magellania*. *Magellania* now contains Recent species from Antarctica, South America, and one from Australia, *Magellania flavescens* (Foster, 1974; Stewart, 1976).

These three genera have similar external features—sculpture, folding, shape, and beak structures. *Magellania* and *Victorithyris* possess the same type of cardinalia (fused socket ridges and crural bases and inner hinge plates only) and differ primarily in that the hinge plates are solid in *Victorithyris*, lamellar and excavate in *Magellania*. The elements of the cardinalia of *Diedrothyris* are lamellar but their form is similar to those Australian and New Zealand species Thomson (1918) attributed to *Stethothyris*, that is, with separate crural bases and socket ridges and inner and outer hinge plates.

All the material described is contained in the collections of the Palaeontology Department, National Museum of Victoria (NMV-P) or in the Ralph Tate Collection, South Australian Museum (SAM-T).

Genus *Victorithyris* Allan, 1940

Type-species: *Victorithyris peterboroughensis* Allan, 1940, by original designation.

Diagnosis: Anterior commissure sulcate to intraplicate; deltidial plates fused; foramen permesothyrid. Cardinalia with fused socket ridges and crural bases, thickened inner hinge

plates meeting on the septum to form a shallow, central trough. Loop teloform.

Stratigraphic range and distribution: Australia: Late Eocene to late Miocene.

Comments: Allan (1940) erected *Victorithyris* for—"Smooth Neothyridinae with permesothyrid foramen, sulcate to intraplicate anterior commissure, magellaniform loop and cardinalia of the *Stethothyris* type" (p. 289). Allan referred to this genus the new species *V. peterboroughensis* and two species, *Magellania pectoralis* and *Magellania sufflata*, which Thomson (1918) had placed in *Stethothyris*. Allan stated that these latter species form "a fairly complete morphological sequence" (p. 293). However, studies of growth stages of the cardinalia of these species demonstrates that they are more closely related to *Stethothyris* than to *Victorithyris*. In *V. peterboroughensis* the socket ridges and crural bases are fused so that inner hinge plates only are present; in *M. pectoralis* and *M. sufflata* there is no fusion of these structures and the crural bases separate inner and outer hinge plates. Accordingly, *M. pectoralis* and *M. sufflata* are returned to the genus *Stethothyris*.

Victorithyris differs from *Magellania* in foraminal position and in the thickness of the components of the cardinalia. *Magellania* is mesothyrid with sulcate folding and lamellar cardinalia; *Victorithyris* is permesothyrid with sulcate to intraplicate folding and thickened cardinalia in adult forms. *Magellania garibaldiana*, *M. divaricata* and *M. tateana* display the foraminal position, folding, and characteristic cardinalia of *V. peterboroughensis*. They are therefore transferred to *Victorithyris*. *Vic-*

torithyris tateana is distinguishable in size, in outline and in beak length from the other three species and is restricted to Late Eocene sediments. *Victorithyris peterboroughensis*, *V. garibaldiana* and *V. divaricata* are a closely related group from the Miocene of southern Australia. *Victorithyris garibaldiana* and *V. peterboroughensis* may be distinguished primarily on presence or absence of plicae and there is a tendency for the plicate species *V. garibaldiana* to display a smaller foramen and a more erect beak than *V. peterboroughensis*. However, the plicae are faint in many specimens of *V. garibaldiana* and in one collection attributed to *V. peterboroughensis* slight plication is evident. Collections of these two species also show similar wide ranges of variation in external features and, in both species, a broadly ovate to subcircular outline is associated with strong folding and a shallowly convex dorsal valve; an ovate outline is associated with moderate or slight folding and a dorsal valve of equal or nearly equal convexity to that of the ventral valve. *Victorithyris garibaldiana* is the dominant brachiopod species in the River Murray Cliffs, *V. peterboroughensis* dominates the Port Campbell Limestone.

A more detailed study of the distribution of the variants of these species would be rewarding. The two species probably arose from a common ancestor in Oligocene or early Miocene times. The large shallow benthic areas of the Murray and Port Campbell Basins apparently provided an environment promoting abundance and diversification. The pattern of variation described above is similar to that evident in populations of living *Magellania flavescens* from different bays of south-eastern Australia (Stewart, 1976). In the Miocene the plicate form (*V. garibaldiana*) came to be characteristic of the Murray River area, the smooth (*V. peterboroughensis*) of the Port Campbell region.

***Victorithyris Peterboroughensis* Allan, 1940**
(Plate 9, figures 1-24)

Victorithyris peterboroughensis Allan, 1940, p. 291, pl. 35, fig. 6, pl. 37, figs. 4-6.

Description: Maximum observed length 44 mm. Outline ovate to subcircular; biconvex, ventral valve strongly convex, dorsal valve moderately convex to flattened with median sulcus extending from the umbonal area. Anterior commissure sulcate to slightly intraplicate; lateral commissures sinuate; cardinal margin moderately curved. Beak suberect to nearly erect.

Dorsal valve with socket ridges and crural bases fused, thick; hinge plates solid, fused laterally with the bases of combined socket ridges and crural bases, medially with each other and the median septum, the median line of fusion visible as a narrow groove, anterior border of hinge plates V-shaped, the median tip being fused with the crest of the septum. Median septum, high, extending approximately the posterior third of total valve length, tapering abruptly anteriorly, thick at line of attachment to valve, free edge sharp. Cardinal process linguiform, posterior surface slightly concave, transversely striated; anterior surface with slightly swollen rim, sloping sharply backwards to fuse with the posterior limits of the hinge plates. Pallial sinuses and adductor muscle scars deeply impressed; anterior adductor scars elongate, flanking anterior half of septum; posterior adductors, elongate, running obliquely from the posterior limit of the septum to the mid-point of the lateral borders of the anterior adductor scars.

Ventral valve with thin shell, lateral walls slightly thickened below small, elongate-ovate hinge teeth; muscle scars not apparent.

Types: National Museum of Victoria—Holotype NMV P15398 (length 30 mm, breadth 23 mm, depth 17 mm); nine hypotypes NMV P52645-52653 from the type locality, collected by E. D. Gill, 19.9.52.

Type locality: Port Campbell Limestone; sea cliffs near monument Peterborough, Victoria (Bairnsdalian).

Stratigraphic range: Bairnsdalian to Cheltenhamian (mid-late Miocene).

Occurrence: South Australia—Bookpurnong Beds (Cheltenhamian); —River Murray Cliffs

south side, 4 km downstream from Loxton.

Victoria—Port Campbell Limestone (Bairnsdalian):—sea cliffs near monument, Peterborough; Two Mile Beach, Port Campbell, top of cliffs at Point Hesse; Hennessy's Steps, top of cliffs 1.6 km east of Sherbrook River; Keilambete; Hopkins River estuary, west bank near Warrnambool; Bay of Islands.

Rutledge's Creek Beds (Bairnsdalian):—Rutledge's Beach, bottom 3.5 m of cliffs; mouth of Rutledge's Creek; Amphitheatre, mouth of Ingle's Creek, 6-15 m above sea level; Sherbrook.

Glenample Clay (Bairnsdalian):—east of Gibson's Steps, Port Campbell Coast; top of cliffs, Gravel Point, 0.8 m west of Gibson's Steps.

Fyansford Clay (Bairnsdalian):—Warrambine Creek, downstream from bridge, near Inverleigh.

Fyansford Formation (Bairnsdalian):—North Shore, Corio Bay.

Tambo River Formation (Mitchellian):—Swan Reach, Tambo River, Gippsland.

Remarks: The holotype with a length of 30 mm is a small adult (Pl. 9, figs. 16-18) consequently illustrations of a larger, more representative, specimen are given here (Pl. 9, figs 7-11).

Specimens attributed to *V. peterboroughensis* from the localities cited above vary in outline, convexity, folding and beak position. Collections from different localities show different ranges of variation in these characters. Attempts to group collections with similar ranges of variation result in the formation of an apparently continuous morphological series with the faunas from Rutledge's Creek Beds at one limit and those from Bookpurnong Beds at the other. Between these two lie the Port Campbell Limestone faunas. Other localities placed in relation to these groups are noted below although some of these are not represented by large numbers of specimens. However, a provisional grouping of this type gives some basis for the further study of faunas in relation to strata (Table 1).

The few intact specimens collected from the Bookpurnong Beds all display plication of late inception near the anterior and lateral margins of the valves. The only character clearly

separating *V. peterboroughensis* and *V. garibaldiana* is the presence of plicae in the latter species. Consequently the attribution of these specimens to *V. peterboroughensis* is made with some doubt; from the existing collection they appear more similar to specimens of *V. peterboroughensis* from Swan Reach and Corio Bay than they are to specimens of *V. garibaldiana* from any locality.

Victorithyris Garibaldiana (Davidson, 1862)
(Plate 10, figures 1-15)

Terebratula sp. Sturt, 1833, p. 254, pl. 3, fig. 15.

Terebratula compta Tenison-Woods, 1862, p. 74, woodcut; *non Terebratula compta* Sowerby, 1845.

Waldheimia garibaldiana Davidson, 1862, p. 446, pl. 24, fig. 9.

Waldheimia imbricata Tenison-Woods, 1865, p. 2, figs 3a-b.

Waldheimia garibaldiana: Etheridge, 1876, pp. 17, 18, pl. 1, figs. 2a, b.

Waldheimia macropora McCoy, 1877, pl. 43, figs. 4, 6.

Waldheimia garibaldiana: Tate, 1880, pp. 146-148, pl. 11, figs 1a-c.

Magellania garibaldiana: Tate, 1899, pl. 252.

Magellania garibaldiana: Thomson, 1927, p. 295.

Description: Maximum observed length 48 mm. Outline ovate to subcircular; biconvex, ventral valve strongly convex with two longitudinal ridges bordering median sulcus, dorsal valve convex to flattened, degree of convexity of the valve being associated with extent and depth of the sulcus, in moderately convex forms the sulcus slight and confined to anterior third of valve, in nearly plane forms sulcus deeper and extending nearly to umbo. Plication, coarse, variable in prominence; in general, marked in bioconvex specimens with ovate outlines and moderate folding, less prominent in those of broader outline, flatter dorsal valves and stronger folding. Anterior commissure sulcate to intraplicate; lateral commissures straight posteriorly, sharply inflected at borders of anterior sulcus; cardinal margin moderately to

TABLE 1

Geographical variants of *Victorithyris peterboroughensis*.

Formation or Locality	Age	External Characters				
		Plicate	Outline	Convexity of dorsal valve	Folding	Beak
Bookpurnong Beds	Cheltenhamian	slight	ovate	moderate	sulcate	erect
Swan Reach	Mitchellian	none	ovate	moderate	sulcate	sub-erect to erect
Corio Bay	Bairnsdalian					sub-erect to erect
Keilambete	Bairnsdalian	none	ovate	slight to moderate	sulcate	sub-erect to erect
Fyansford Clay	Bairnsdalian					sub-erect to erect
Hopkins River	Bairnsdalian	none	ovate to broadly ovate	slight to moderate	sulcate	sub-erect to erect
Port Campbell Limestone	Bairnsdalian					sub-erect to erect
Glenample Clay	Bairnsdalian	none	ovate to broadly ovate	slight	sulcate to intraplicate	sub-erect
Rutledge's Creek Beds	Bairnsdalian	none	broadly ovate	slight to flat	strongly sulcate to intraplicate	sub-erect

strongly curved. Broad shell outline and intraplicate folding generally associated with larger specimens (length range 35-40 mm). Beak suberect to erect; foramen small.

Types: British Museum (Natural History)—Holotype B4982; National Museum of Victoria—Syntype NMV P12183 of *Waldheimia macropora* McCoy, Flemington, Victoria; seven hypotypes (NMV P52654-52660) from the Morgan Limestone, Murray River Cliffs, collected by F.A. Cudmore.

Type locality: Mount Gambier Limestone (Longfordian) Mount Gambier, South Australia.

Stratigraphic range: Longfordian to Cheltenhamian (early to late Miocene).

Occurrence: South Australia—Morgan Limestone, Lower Member (Longfordian), Murray

River Cliffs. Morgan Limestone, Cadell Marl Lens (Balcombian), Murray River Cliffs. Morgan Limestone, Upper Member (Balcombian), Murray River Cliffs.

Mount Gambier Limestone (Longfordian), Mount Gambier.

Tasmania—Freestone Cove Sandstone (Longfordian), Table Cape.

Victoria—Bairnsdale Limestone (Bairnsdalian): Neumerella, Drier's lower beds, Mitchell River, Pound Swamp, Mitchell River.

Balcombe Clay (Balcombian):—Balcombe Bay; Grice's Creek; Mount Eliza.

Fyansford Formation (Balcombian):—Orphanage Hill, Geelong; Red Hill, Shelford.

Gellibrand Marl (Batesfordian):—cutting on Bornong Road, north of Cooriemungle Road.

Gippsland Limestone (Bairnsdalian):—railway cutting 1.6 km west of Orbost.

Muddy Creek Marl (Balcombian):—Clifton Bank, Muddy Creek.

Puebla Clay (Longfordian):—Birregurra, left

bank Barwon River.

Sandringham Sands (Cheltenhamian):—Beaumaris.

Remarks: Davidson (1862) erected the species from a specimen believed to have been collected from the Tertiary beds of Malta. Subsequently Etheridge (1876) noted that Davidson himself was satisfied (from an examination of the matrix filling the valves) that the specimen came from the coralline Limestone of Mount Gambier, South Australia. In 1880 Tate reviewed the species and referred to it a large collection of specimens from the River Murray Cliffs. Tate noted the variability of this collection and placed in the synonymy of *V. garibaldiana* three species, all with characters lying within the range of variation of the collection from the River Murray Cliffs. *Terebratula* sp. Sturt from the Murray River and *Waldheimia imbricata* Tenison-Woods from Mount Gambier were considered by Tate to be adolescent forms while the type of *Waldheimia macropora* McCoy from Flemington, Victoria, displays a form common in collections from the River Murray Cliffs. Tenison-Woods (1878) referred specimens collected at Table Cape, Tasmania to *W. imbricata*. These specimens are presumed to have been lost but Tenison-Wood's illustrations bear a similarity to the new species *Diedrothyris plicata* although *V. garibaldiana* also occurs at Table Cape.

Only one broken specimen from the type locality is available in the collections of the National Museum of Victoria and the South Australian Museum, consequently the species is redescribed from material collected by F. A. Cudmore from the Murray River Cliffs. Specimens in this collection resemble closely Davidson's and Etheridge's illustrations of the species. The Murray River Cliffs are the most prolific sources of *V. garibaldiana*. Collections from some beds in these cliffs are characterised by a wider range of variation in external features than is known from other localities. Further collections need to be made in this area for any relationship between variation and different strata to be established. F. A. Cudmore's collections from the Lower Member of the Morgan Limestone show the full range of

variation described for the species while specimens in collections from the Cadell Marl Lens and the Upper Member are broadly ovate with a flattened dorsal valve and pronounced folding. The other extreme in the range of variation noted for the species (narrowly ovate outline, convex dorsal valve, slight folding) characterises specimens from a lower horizon, the Mannum Formation—they are attributed to *V. divaricata*.

Collections of *V. garibaldiana* from other localities cited are generally too small to give ranges of variation. Some, however, show sufficient consistency to be noteworthy, for example those specimens obtained from Beaumaris, Victoria, are relatively small in size (maximum observed length 25 mm) with slightly convex valves and plicae confined to the valve margins; specimens from Table Cape, Tasmania, all display prominent multiplication extending from the umbo to the valve margins.

***Victorithyris divaricata* (Tate, 1880)**

(Plate 10, figure 16)

Waldheimia (?) *divaricata* Tate, 1880, p. 149, pl. 8, figs. 8a-b.

Types: South Australian Museum—Lectotype T868E (length 26 mm, breadth 20 mm, depth 13 mm), Tate's figure 8, Paralectotypes T868A-D, F, G, Ralph Tate Collection.

National Museum of Victoria—Hypotype NMV P52661 F. A. Cudmore Collection.

Type locality: Mannum Limestone (early Miocene); red raggy limestone, Mannum, River Murray, South Australia.

Stratigraphic range: Early Miocene.

Occurrence: South Australia—Mannum Formation (early Miocene):—lower beds at Swan Reach, Wongulla and Morgan to Mannum, River Murray Cliffs.

Remarks: Tate (1880) noted the similarity between *V. divaricata* and *V. garibaldiana* but considered that the former species displayed a narrow shell, a less inflated dorsal valve,

broadener deltidial plates and more conspicuous beak ridges than *V. garibaldiana*. These external features are evident in some specimens from the highly variable collections of *V. garibaldiana* from the white calcareous beds near Morgan (Tate's references, Bed No. 9). Consequently the two species differ in their ranges of variation, that of *V. garibaldiana* being wide and incorporating the narrower range of variation apparent in collections of *V. divaricata*. *V. divaricata* is retained with doubt and until further collections are made from the River Murray Cliffs.

***Victorithyris tateana* (Tate, 1880)**

(Plate 11, figures 1-8)

Waldheimia tateana Tate, 1880, p. 150, pl. 7, figs 6 a-b, pl. 8, fig. 6a-c, pl. 9, fig. 2.

Magellania tateana Tate, 1899, p. 253.

Description: Small to moderate in size (maximum observed length from the type locality, 24 mm); outline narrowly ovate to pyriform; anterior commissure sulcate or slightly intraplicate, the folding of late inception, specimens less than 20 mm in length being rectimarginate or shallowly sulcate; lateral commissures rectimarginate; cardinal margin strongly curved; beak suberect, foramen small. Dorsal and ventral valve interior structures agree with those of the type species.

Types: South Australian Museum—Lectotype SAM T906J, Paralectotypes T906A-H, Ralph Tate Collection.

National Museum of Victoria—Hypotypes, NMV P52662, P52663, F. A. Cudmore Collection.

Type locality: Tortachilla Limestone (Aldingan): Maslin Bay, Aldinga, South Australia.

Stratigraphic range: Aldingan (late Eocene-early Oligocene).

Occurrence: South Australia—Tortachilla Limestone; Port Noarlunga; Stansbury on Yorke Peninsula; Aldinga Bay.

Victoria—Castle Cove Limestone:—Wilkinson's Locality 5, Grid No.

307162; Calder River Limestone:—anticline on Aire Coast, near Middle Beach, Glen Aire.
Glen Aire Clays:—Wilkinson's reference Locality 1, Point Flinders, Cape Otway.

Remarks: The largest collection of specimens available (total 47) is from the type locality. Other localities cited are represented by less than ten, usually broken, specimens, consequently differences may exist between populations which are not apparent in such small samples.

***Diedrothyris* gen. nov.**

Derivation: diedros Gr. = sitting apart.

Type species: *Waldheimia* (?) *johnstoniana*, Tate, 1880

Diagnosis: Anterior commissure rectimarginate to sulcate to intraplicate; deltidial plates, short, fused; foramen mesothyrid; shell commonly plicate. Cardinalia with crural bases separating excavate inner and outer hinge plates. Loop teliform.

Stratigraphic range and distribution: Australia. Late Eocene-mid Miocene.

Comments: The species now assigned to *Diedrothyris* were formerly included in the genus *Waldheimia* = *Magellania*. These species resemble *Magellania* in external features, i.e., plication, curvature of the cardinal margin, beak and foraminal condition, but differ from the genus in the possession of outer hinge plates. In *Magellania* the socket ridges and crural bases are fused and excavate, inner hinge plates extend from them medially to fuse on top of the septum. In *Diedrothyris* the crural bases separate inner and outer hinge plates, the outer hinge plates lying between the socket ridges and the crural bases. *Stethothyris* displays a similar cardinalia pattern. However, in this genus the hinge plates are solid in adult forms and plication seen to some degree in all members of *Diedrothyris*, is absent. Furthermore, the Australian members of *Stethothyris* display a small, permesothyrid foramen with an erect to

incurved beak. Species included in *Diedrothyris* display a suberect beak and a foramen of moderate size which is mesothyrid. Other species showing affinities with *Diedrothyris* are *Magellania joubini* Blochmann and *Magellania fragilis* Smith. In these species crural bases separate inner and outer hinge plates and the loop is teloform. Externally, *Diedrothyris furcata* is almost indistinguishable from *Gyrothyris mawsoni* Thomson while *Diedrothyris plicata* is similar to *Magellania flavesces*.

The three species assigned to *Diedrothyris* differ externally in folding and plication, internally in the shape of the cardinal process and in the position at which the inner hinge plates lies in relation to the crural bases. The cardinal process is rectangular in outline in *D. johnstoniana* and *D. furcata*; in *D. plicata* the cardinal process is narrow and transverse. The hinge plates and the crural bases form a level horizontal platform in *D. johnstoniana* and *D. plicata*; in *D. furcata* the socket ridges are elevated and the hinge platform medially depressed owing to the fact that inner hinge plates extend medially from the lower and not the upper borders of plate-like crural bases. With respect to the folding of the anterior commissure, *D. furcata* is rectimarginate, *D. johnstoniana* varies from rectimarginate to sulcate to intraplicate, and *D. plicata* from sulcate to intraplicate. The valves of *D. furcata* and *D. plicata* are entirely plicate; in *D. johnstoniana* the plicae are confined to the margins of the anterior halves of the valves.

***Diedrothyris johnstoniana* (Tate, 1880)**
(Plate 11, figures 9-16)

Waldheimia (?) *johnstoniana* Tate, 1880, p. 151, pl. 8, figs 9a-b.

Waldheimia (?) *fimbriata* Tate, 1880, pp. 150-151, pl. 8, figs 2a-b.

Magellania johnstoniana: Tate, 1899, p. 253.

Magellania (?) *fimbriata*: Tate, 1899, p. 252.

Magellania (?) *fimbriata*: Thomson, 1927, p. 295.

Description: Maximum observed length 29 mm. Outline subpentagonal, anterior margin

straight, greatest width at mid-length; biconvex, ventral valve deeper. Plication coarse, variable in prominence, restricted to anterior regions only. Anterior commissure intraplicate; lateral commissures straight; cardinal margin strongly curved. Beak short, suberect.

Socket ridges, low, moderately stout, converging slightly posteriorly to fuse with dorsal umbo borders. Crural bases linear posteriorly, widening and diverging slightly anteriorly. Outer hinge plates excavate, narrow, fused laterally with socket ridges, medially with crural bases. Inner hinge plates, excavate, fused laterally with crural bases, medially with each other and crest of median septum, anterior border deeply V-shaped. Median septum blade-like, short. Cardinal process small, rectangular in outline. Muscle and pallial impressions not visible.

Ventral valve with thin shell; rectangular hinge teeth without swollen bases. Muscle impressions not visible.

Types: South Australian Museum—Lectotype T867A, Paralectotypes T867B-F, T871A-H, J. Ralph Tate Collection.

National Museum of Victoria—Hypotypes P52664-P52665, collection of J. R. Richardson. **Type locality:** Tortachilla Limestone (Aldingan): Maslin Bay, Aldinga, South Australia.

Stratigraphic range: Aldingan (late Eocene).

Remarks: Tate's species *Waldheimia fimbriata* and *W. johnstoniana* agree in all internal and external features except size, outline, and the prominence and extent of plication. Collections made at the type locality of both species (Tortachilla Limestone, Maslin Bay, Aldinga, S. A.) show that the two species are linked by a series of intermediate forms and that the specimens designated *W. fimbriata* are juvenile forms of *W. johnstoniana*.

The specimen of *W. fimbriata* figured by Tate (No. T871B, in the Tate Collection, South Australian Museum) is the largest (23 mm in length) specimen in his collection of nine syntypes. This specimen is ovate in outline with prominent anterior plication (which does not extend beyond the mid-length of the valves) and

with a rectimarginate anterior commissure. The remaining syntypes vary in the prominence and extent of plication and in the folding of the anterior commissure. The prominent and regular plication displayed in Tate's syntype (Tate, 1880, pl. 8, figs 2a-b) is not characteristic of these specimens in which the sculpture is more in the nature of irregularly spaced plicae confined to the areas immediately adjacent to the margins of the valves. The anterior commissure varies between rectimarginate and slightly intraplicate. The lectotype of *D. johnstoniana* (pl. 11, figs 15-16) is 6 mm longer than the figured syntype of *D. fimbriata* and the former species is subpentagonal in outline. However it is apparent from the growth lines on this specimen of *D. johnstoniana* that, at a growth stage of a size equivalent to that of *D. fimbriata*, it displayed an ovate outline.

***Diedrothyris furcata* (Tate, 1880)**

(Plate 11, figures 17-19)

Waldheimia furcata Tate, 1880, pp. 148-149, pl. 7, figs 2a-b.

Magellania furcata Tate, 1899, p. 252.

Magellania furcata: Thomson, 1927, p. 295.

Description: Maximum observed length 22 mm. Outline ovate; biconvex. Multiplicate, plicae arising immediately anterior to umbo, anteriorly plicae widen and bifurcate. Lateral and anterior commissures straight; cardinal margin strongly curved. Beak short, suberect; foramen small.

Socket ridges elevated, moderately stout, converging slightly posteriorly to fuse with dorsal umbo borders. Crural bases, narrow vertical plates, separating inner and outer hinge plates. Outer hinge plates, excavate, fused laterally with bases of socket ridges, medially with upper borders of crural bases. Inner hinge plates, excavate, fused laterally with lower borders of crural bases, medially with each other and the crest of the median septum; anterior border deeply V-shaped. Cardinal process small, rectangular, posterior border attached to umbo, lateral and anterior borders free. Muscle and

pallial impressions not visible. Ventral valve interior as for type-species.

Types: South Australian Museum—Lectotype T865A (length 22 mm, breadth 18 mm, depth 15 mm), paralectotypes T865B-E, Ralph Tate Collection.

National Museum of Victoria—Hypotype, P52666, collection of J. R. Richardson.

Type locality: Port Willunga Formation, south of Port Willunga, Aldinga, South Australia.

Stratigraphic range: Late Oligocene to early Miocene.

Occurrence: Formation unknown:—Surveyor's Point, Yorke Peninsula, South Australia.

***Diedrothyris plicata* sp. nov.**

(Plate 11, figures 20-25)

Magellania garibaldiana Pritchard, 1910, p. 90, fig. 20.

non Victorithyris garibaldiana (Davidson, 1862)

Magellania garibaldiana: Gill and Baker, 1955, pp. 39-43, pl. 1, fig. 1.

non Victorithyris garibaldiana (Davidson, 1862)

Derivation: *plicatus* L. = folded

Description: Maximum observed length 32 mm. Outline subpentagonal, greatest breadth slightly anterior to mid-length; unequally biconvex, ventral valve deeper and carinate, dorsal valve slightly depressed medially by shallow anterior sulcus. Multiplicate, two primary plicae lying within the dorsal valve sulcus and the ventral carina; four primary plicae on lateral commissure sinuate; cardinal margin strongly curved. Foramen, large; beak suberect. Muscle and pallial impressions not visible.

Socket ridges low, converging posteriorly to fuse with dorsal umbo anteriorly overhanging triangular sockets, laterally fused with outer hinge plates, the two structures forming gently sloping surfaces. Crural bases, vertical plates, diverging anteriorly; outer and inner hinge

plates attached to upper borders so that the three structures form a T-shaped cross-section, the vertical formed by crural bases, outer and inner hinge plates forming each side of horizontal. Hinge plates, lamellar, excavate, almost horizontal; inner hinge plates fused medially within median septum; anterior border low V-shape. Cardinal process narrow, transverse. Muscle and pallial impressions not visible. Ventral valve as for type-species.

Types: National Museum of Victoria—Holotype, P17366 (length 27 mm, breadth 19 mm, depth 15 mm); paratypes P173677-8, F. A. Cudmore Collection; Hypotypes P15324, Pritchard Collection; P16826, E. D. Gill Collection; P12183, McCoy Collection.

Type locality: Freestone Cove Sandstone (early Miocene); Lower beds, Table Cape, Tasmania. Stratigraphic range: Late Oligocene to middle Miocene.

Occurrence: Tasmania—Cape Grim Beds (early Miocene);—Cape Grim.

Victoria—Batesford Limestone (early Miocene);—Batesford Filter Quarries.

Muddy Creek Marl (middle Miocene);—Clifton Bank, Muddy Creek.

Point Addis Limestone (late Oligocene);—Airey's Inlet, Waurin Ponds.

Formation unknown (middle Miocene);—Cr. Hoffman Road and Buckley Street, Aberfeldie; Flemington; Royal Park Railway Cutting, Melbourne.

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Explanation of Plates

PLATE 9

Victorithyris peterboroughensis Allan

- Figs. 1-5— Hypotype P52649, dorsal, ventral, lateral, anterior and posterior views, $\times 0.75$. Rutledge's Creek Beds. Rutledge's Beach. Bottom 3.5 m of cliffs, Victoria.
Fig. 6— Hypotype P52650, dorsal interior, $\times 1.5$. Rutledge's Creek Beds. Rutledge's Beach, bottom 3.5 m of cliffs, Victoria.
Figs. 7-11— Hypotype P52645, dorsal, ventral, lateral, anterior and posterior views, $\times 1$. Port Campbell Limestone, sea cliffs near monument, Peterborough, Victoria.
Fig. 12— Hypotype P52646, dorsal interior, $\times 2$. Port Campbell Limestone, sea cliffs near monument, Peterborough, Victoria.

- Fig. 13 Hypotype P52647, dorsal interior, $\times 4$, Port Campbell Limestone, sea cliffs near monument, Peterborough, Victoria.
- Fig. 14 Hypotype P52648, dorsal interior, $\times 2$, Port Campbell Limestone, sea cliffs near monument, Peterborough, Victoria.
- Fig. 15 Hypotype P52653, dorsal interior, $\times 2$, Port Campbell Limestone, sea cliffs near monument, Peterborough, Victoria.
- Figs. 16-18 Holotype P15298, dorsal, lateral and anterior views, $\times 1.2$, Port Campbell Limestone, sea cliffs near monument, Peterborough, Victoria.
- Figs. 19-23 Hypotype P52651, dorsal, ventral, lateral views, anterior and posterior views, $\times 1$, Bookpurnong Beds, south bank, River Murray, downstream from Loxton, South Australia.
- Fig. 24 Hypotype P52652, dorsal interior, $\times 1.5$, Bookpurnong Beds, south bank, River Murray, 4 km downstream from Loxton, South Australia.

PLATE 10

Victorithyris garibaldiana (Davidson)

- Fig. 1 Hypotype P52654, dorsal view $\times 0.9$, Morgan Limestone, Upper Member, hard yellow limestone, Tate's reference beds, Nos 3-5, Murray River Cliffs, South Australia.
- Fig. 2 Hypotype P52654, ventral view, $\times 1$, Morgan Limestone, Upper Member, hard yellow limestone, Tate's reference beds, Nos 3-5, Murray River Cliffs, South Australia.
- Figs. 3-5 Hypotype P52654, lateral, anterior and posterior views, $\times 1$, Morgan Limestone, Upper Member, hard yellow limestone, Tate's reference beds, Nos 3-5, Murray River Cliffs, South Australia.
- Figs. 6-10 Hypotype P52655, dorsal, ventral, lateral, anterior and posterior views, $\times 1$, Morgan Limestone, Upper Member, hard yellow limestone, Tate's reference beds, Nos 3-5, Murray River Cliffs, South Australia.
- Fig. 11 Hypotype P52656, dorsal views, $\times 1$, Morgan Limestone, Upper Member, hard yellow limestone, Tate's reference beds, Nos 3-5, Murray River Cliffs, South Australia.
- Fig. 12 Hypotype P52657, dorsal view, $\times 1$, Morgan Limestone, Upper Member, hard yellow limestone, Tate's reference beds, Nos 3-5, Murray River Cliffs, South Australia.
- Fig. 13 Hypotype P52659, dorsal view, $\times 1$, Morgan Limestone, Upper Member, hard yellow limestone, Tate's reference beds, Nos 3-5, Murray River Cliffs, South Australia.
- Fig. 14 Hypotype P52658, dorsal view, $\times 1$, Morgan Limestone, Upper Member, hard yellow limestone, Tate's reference beds, Nos 3-5, Murray River Cliffs, South Australia.

- Fig. 15 Hypotype P52660, dorsal interior view, $\times 1$, Morgan Limestone, Upper Member, hard yellow limestone, Tate's reference beds, Nos 3-5, Murray River Cliffs, South Australia.

Victorithyris divaricata (Tate)

- Fig. 16 Hypotype P52661, dorsal view, $\times 1.5$, Mannum Limestone, red raggy limestone, Mannum, Murray River Cliffs, South Australia.

PLATE 11

Victorithyris lateana (Tate)

- Figs. 1-2 Lectotype T906J, dorsal and lateral views, $\times 1.5$.
- Figs. 3-4, 6-8 Hypotype P52662, dorsal, ventral, lateral, anterior and posterior views, $\times 1.5$, Tortachilla Limestone, Maslin Bay, Aldinga, South Australia.
- Fig. 5 Hypotype P52663, dorsal interior view, $\times 2.3$, Tortachilla Limestone, Maslin Bay, Aldinga, South Australia.

Diedrothyris johnstoniana (Tate)

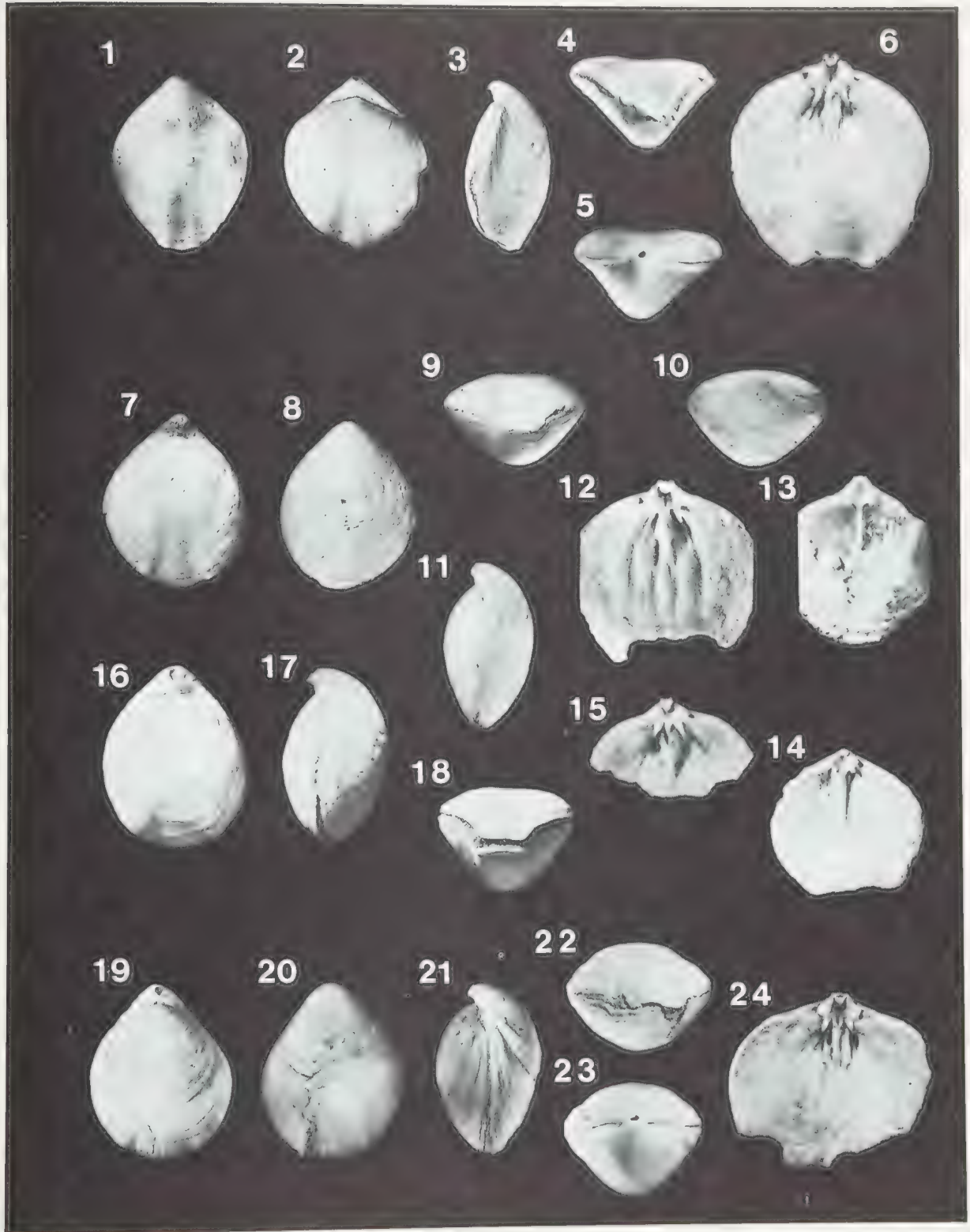
- Figs. 9-13 Hypotype P52664, dorsal, ventral, lateral, anterior and posterior views, $\times 1.6$, Tortachilla Limestone, Maslin Bay, Aldinga, South Australia.
- Fig. 14 Hypotype P52665, dorsal interior view, $\times 2$, Tortachilla Limestone, Maslin Bay, Aldinga, South Australia.
- Figs. 15-16 Lectotype T867A, dorsal and lateral views, $\times 1.2$.

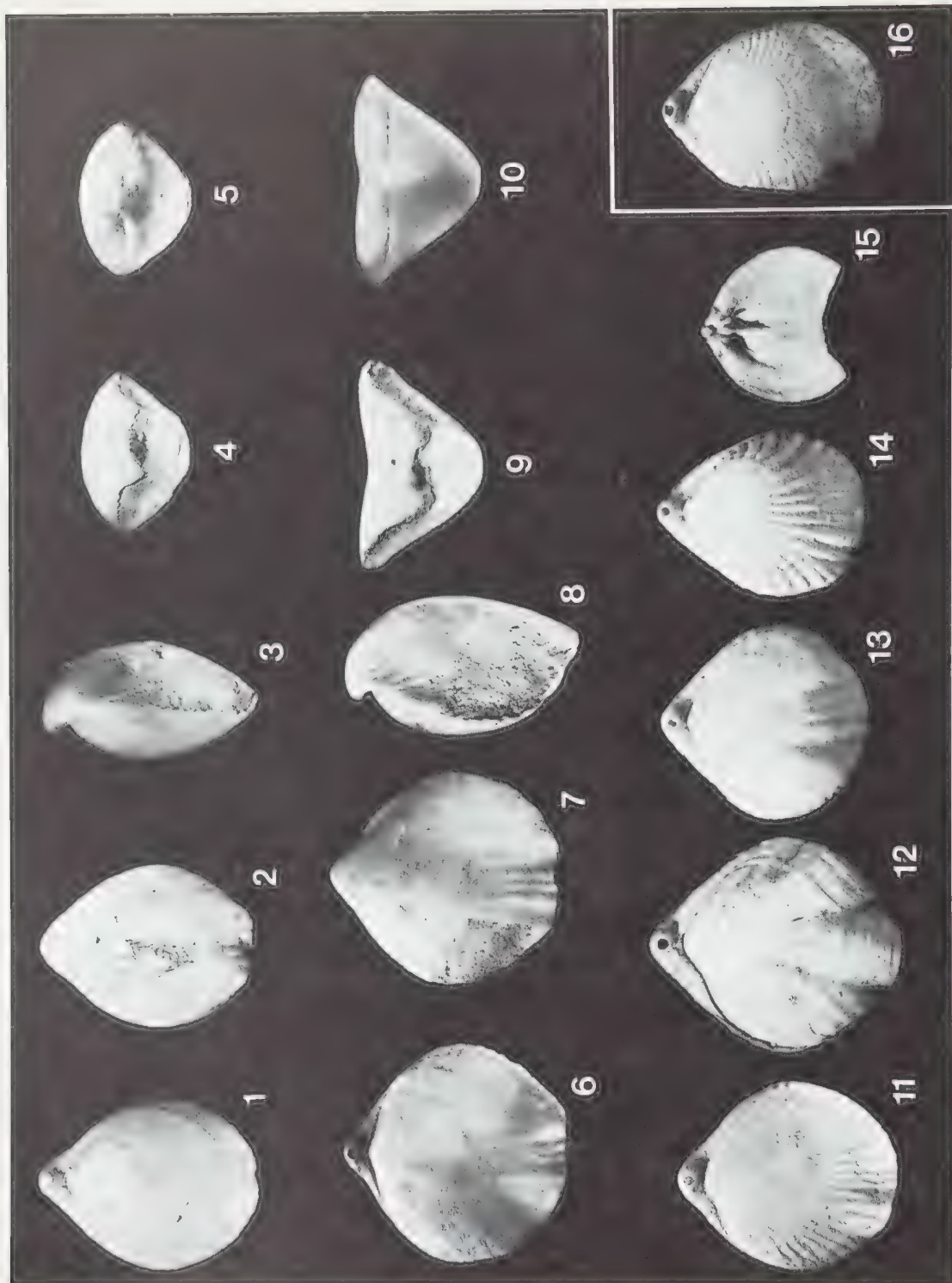
Diedrothyris furcata (Tate)

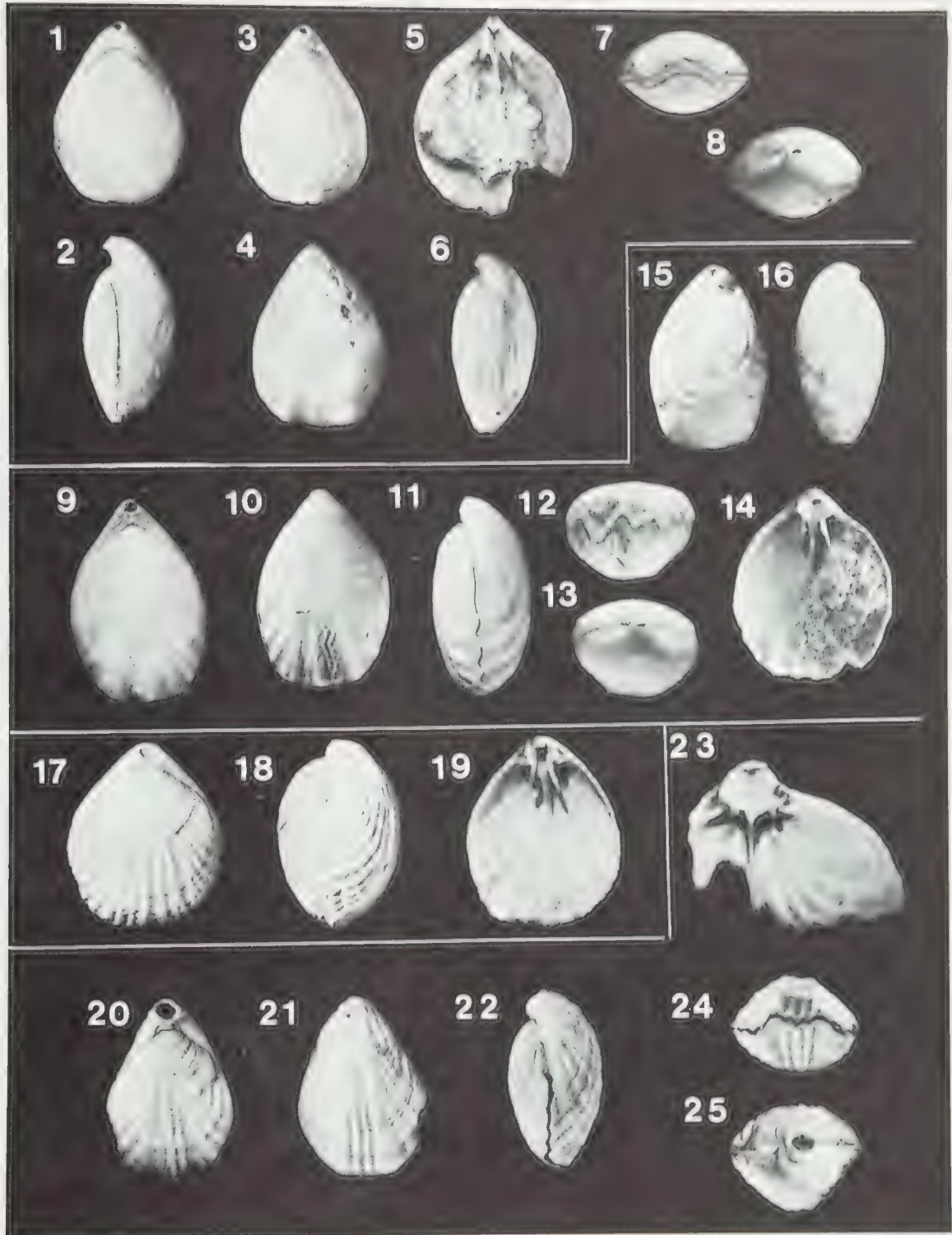
- Figs. 17-18 Lectotype T865A, dorsal and lateral views, $\times 1.5$, Port Willunga Formation, south of Port Willunga, Aldinga, South Australia.
- Fig. 19 Hypotype P52666, dorsal interior view, $\times 2.2$, Port Willunga Formation, south of Port Willunga, Aldinga, South Australia.

Diedrothyris plicata sp. nov.

- Figs. 20-22 Holotype P17366, dorsal, ventral, lateral views, $\times 1.3$, Freestone Cove Sandstone, lower beds, Table Cape, Wynyard, Tasmania.
- Fig. 23 Paratype P17367, dorsal interior view, $\times 3$, Freestone Cove Sandstone, lower beds, Table Cape, Wynyard, Tasmania.
- Figs. 24-2 Holotype P17366, anterior and posterior views, $\times 1.3$, Freestone Cove Sandstone, lower beds, Table Cape, Wynyard, Tasmania.







THE IDENTITY OF TWO TUBULARIAN HYDROIDS FROM AUSTRALIA WITH A DESCRIPTION AND OBSERVATIONS ON THE REPRODUCTION OF *RALPHARIA MAGNIFICA* gen. et sp. nov.

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Abstract

The identity of two common Australian tubularian hydroids is established. *Tubularia ralphi* Bale is an estuarine species and an important component of the summer fouling communities in Australian ports. *T. ralphi* has been recorded under various synonyms from southern Australia.

Ralpharia magnifica gen. et sp. nov. is described. It is a widely, although sparsely distributed species on shallow oceanic and sheltered water reefs in southern Australia. It has formerly been confused with *T. ralphi* Bale.

Ralpharia releases a free-swimming, short-lived medusa with 4 tentacle knobs and 4 radial canals. Nematocyst tracks are absent. The amoeboid egg, growth of the actinula and late development of the oral tentacles of the young hydranth indicate a close relationship with the primitive Athecata.

Introduction

The literature on Australian tubularian hydroids is confused, some species having been poorly described in the past from inadequate material, leading to misidentifications by later workers, while the literature as a whole is in need of revision (Watson, 1979).

The identity of the two most abundant and widely distributed Australian species of *Tubularia* is discussed in this paper.

Ralph (1966) recorded two species of *Tubularia* collected from four localities (Point Cook, Mud Islands, off Sandringham and near Port Phillip Heads) in the Port Phillip Survey, 1957-1963. The taller species with stems 10 cms high, collected from the two latter localities, she assigned to *Tubularia ralphi* Bale, 1884, remarking that this "tall stemmed tubularian possesses characters similar to that described by Bale (1884) for specimens from Port Phillip, and by other workers (Broch, 1948) for *T. ralphi* Bale". She tentatively assigned the smaller hydroid with clustered stems up to 4 cm high to *Tubularia larynx* Ellis & Solander, 1786, as the first record of the species from Australia. The colonies of both hydroids were moribund at the time of collection.

Bale (1884) gave a very brief description of "*T. ralphi* Halley m.s." after a description of the species read before the Microscopical Society of Victoria by Halley in 1879. Halley's description was not subsequently published, nor was any record of the paper kept in the Society's archives. Search of the hydroid collections of the National Museum, Melbourne, and

the Australian Museum, Sydney failed to reveal any specimens. In his description of *T. ralphi*, Bale makes particular reference to the habitat of this hydroid in Hobsons Bay, remarking that it is "common on piles, ships, etc."

During ecological studies extending over several years in Hobsons Bay, the author observed colonies of a tubularian hydroid seasonally very abundant on wharves and port beacons near the mouth of the Yarra River where it enters Hobsons Bay. Colonies of this hydroid so closely resemble Bale's description of the "stems clustered, three or four inches in height, slender, . . . smooth or obscurely wrinkled transversely, simple or rarely branched; polypites about one-third of an inch across the tentacles . . . Gonophores in clusters on branched peduncles; ovate, with four small tubercles at the summit, and a small aperture" that there is no doubt that this hydroid is *T. ralphi*. Careful search among the epibiota of Hobsons Bay has failed to find evidence of any other tubularian hydroid which answers this description. Examination of a large range of fresh material of this hydroid shows that the four small tubercles on the gonophores, mentioned by Bale, are apical crests, fugitive structures which occur on only a few of the male gonophores. Later authors have assumed that these were perradial tentacle knobs, present on the gonophores of both sexes of some tubularian species.

Lendenfeld (1885) described *Tubularia gracilis* from the "Laminarian Zone" at Port Jackson, New South Wales. Thornely (1904),

recognised material from Ceylon as *T. gracilis*. Fenchel (1905) considered *T. gracilis* to be synonymous with *T. larynx*. Stechow (1925) recorded *T. gracilis* from the mouth of the Swan River, Western Australia, renaming it *T. australis* because of pre-occupation of the name *T. gracilis* Harvey, 1836.

I have examined Lendenfeld's specimens of *T. gracilis* in the collection of the Australian Museum. The spirit preserved specimens labelled "G10801 Type" are too poorly preserved for detailed examination but another specimen labelled "G10800 Port Jackson, New South Wales" is well preserved. This material is conspecific with *T. ralphi* from Hobsons Bay.

Hickson & Gravely (1907) assigned a group of dead perisarcal tubes 60-120 mm high and a single hydranth "not well preserved, as well as a few immature specimens" from McMurdo Bay, Antarctica, to *T. ralphi*. Their material had "long slender hydrocauli arising from a contorted hydrorhizal plexus". Following Hickson & Gravely, Broch (1948) assigned a moderately tall stemmed hydroid from Peter I Island, Antarctica, to *T. ralphi*, remarking that his two specimens were solitary but with some evidence of there having been a hydrorhiza. The hydrocauli were feebly striated throughout their length and the hydranths had about 25 aboral and 30-40 oral tentacles. It is virtually impossible to assign tubularian hydroids to species in the absence of fertile parts, and from their description it is very doubtful that the material of these authors was indeed *T. ralphi*.

More recently, Ewer (1953) described a new species, *Tubularia warreni* from the coast of Natal, South Africa. His detailed description, particularly of the cnidome, leaves no doubt that *T. warreni* is synonymous with *T. ralphi*.

Pennycuik (1959) doubtfully assigned an immature hydroid from Moreton Bay, Queensland, to *Tubularia crocea* (Agassiz, 1862), as the first record of this species from Australian waters. *T. crocea* is known from the Atlantic and Pacific coasts of the U.S.A. (Agassiz, 1862; Torrey, 1902; Fraser, 1944; Calder, 1970), and from Christmas Island in the Indian Ocean (Ritchie, 1910). Specimens of *T. ralphi* collected from ports and estuaries along the Australian coastline from Gladstone,

Queensland, to Fremantle in Western Australia very closely resemble specimens of *T. crocea* from Chesapeake Bay, U.S.A., provided by Dr. D. Calder. The cnidome of *T. crocea* has atrichous isorhizas (Weill, 1934) while *T. ralphi* has abundant heterotrichous anisorhizas. Only examination of the nematocysts of fresh material of each will determine whether the two are indeed conspecific. In the meanwhile, the species are considered separate.

Since there is no existing type material of *T. ralphi* it is necessary to erect a neotype. A typical colony from Bale's original locality at the mouth of the Yarra River in Hobsons Bay is nominated as the neotype. A description of *T. ralphi* from the neotype colony is given later in this paper.

Referral of the specimens identified by Ralph (1966) as *T. larynx* to *T. ralphi* leaves the tall stemmed tubularian from Port Phillip Bay without identity. This hydroid is common on sheltered ocean reefs and in clear water embayments along the southern and south-eastern coastline, and because of its large size and graceful hydranths it is often photographed by divers. The distribution, ecology and reproduction of this hydroid has been investigated by the author. Certain features of the structure and release of the medusae and early larval development are unique among the Tubulariidae, warranting the erection of a new genus.

Type material on which the following descriptions are based is lodged in the National Museum of Victoria, Melbourne (NMV).

Ralpharia gen. nov.*

Diagnosis: Hydranths colonial, hydrocaulus with firm perisarc, gonophores released as free swimming medusae. Medusae radially symmetrical with four radial canals and four rudimentary marginal tentacles. Nematocyst tracks absent.

Ralpharia magnifica sp. nov.

Type Material: Holotype, NMV G3224; paratypes G 3225, G 3226.

* Named for Dr. P. M. Ralph who first recorded this hydroid and who has contributed much to understanding of the Trans-Tasman hydroid fauna.

Material preserved in 5% formalin. Coll: J. E. Watson, 3/1/79 from reef at Tortoise Head, Western Port, 2 m deep, on the alcyonacean *Parerythropodium membranaceum* Kükenthal, 1906. Description from holotype and paratypes: Colonies sparse, comprising a few to 20 erect stems arising from a tubular hydrorhiza embedded in the sheet-like mass of the alcyonacean. Diameter of hydrorhiza up to 1 mm. Stems to 150 mm high and 2-2.5 mm diameter at widest part immediately below hydranth. Perisarc of stems thick and smooth, very thick on the hydrorhiza, thinning distally, the perisarc of the distal region 4-5 mm below hydranth reduced to a transparent transversely wrinkled sheath. (In preserved material the coenosarc of this region of the stem is contracted to a narrow cylinder which expands distally into a thin collar supporting the hydranth; in life, the coenosarc in this part of the stem is inflated, filling the entire upper stem cavity). In transverse section, stems comprise a thin, transparent outer pellicle overlying the thick perisarc layer; internally, the walls are lined with a ring of numerous, small, subcircular canals, one of which is always 3-4 times the diameter of the others (Fig. 2). These longitudinal canals are clearly visible through the distal stem wall where the perisarc is thin. In the lower stem region and hydrorhiza, the canal system fills much of the stem cavity, but distally the canals lie close to the wall, the core of the stem being occupied by a mass of parenchymous cells.

Hydranths large, in life up to 50 mm across the extended tentacles. Aboral tentacles 27-40 in number, up to 30 mm long, arranged in a single verticil and up to 150 oral tentacles 1-5 mm long, bunched in a dense tuft 5-6 rows deep around the mouth; a few very short tentacles less than 1 mm long usually present around the basal row of oral tentacles. Body of hydranth 4-5 mm in diameter and 3-4 mm in length between the basal row of oral tentacles and the blastostyles (preserved material), and finely, but conspicuously striated. Internally, the endoderm of the gastral cavity comprises an upper, deeply lobed layer, and a lower, dark coloured band of digestive glands.

Blastostyles numerous, 50-60 arising in a

circlet 2-3 deep proximal to the oral tentacles, mature blastostyles up to 5 mm long, much branched, bearing up to 8 mature or nearly mature gonophores and many immature gonophores in various stages of development. When fully fertile, the proximal blastostyles tend to droop in clusters between the tentacles. Gonophores of both sexes identical in shape and size but borne on different hydranths, attached to blastostyle by a short wrinkled pedicel.

Medusa at liberation about 2.5 mm long and 0.8-1 mm wide with 4 radial canals and 4 poorly developed inter-radial ribs and 4 rudimentary tentacle knobs. Jelly moderately thick with a well developed shelf-like velum and a simple, circular opening surrounded by a raised internal collar. Nematocysts rare on exumbrella but concentrations of large anisorhizas present on tentacle knobs. Spadix simple, about half to two-thirds length of the medusa, varying in shape from oval to conical, without mouth or stomach. At release, the gonads completely surround the spadix, occupying most of the internal cavity, the female medusa containing 12-18 eggs.

Nematocysts of four kinds present:

- Hydranth —(i) moderately abundant stenoteles with round capsule, 10×10 - $14 \times 14 \mu$ (Fig. 4).
 —(ii) very abundant stenoteles with elongate capsule, 7×5 - $9 \times 7 \mu$ (Fig. 5).
 —(iii) very rare ? isorhizas, undischarged, capsule 15×16 - $17 \times 17 \mu$ (Fig. 6).

Gonophores —

- (i) very abundant? isorhizas, capsule $8 \times 3 \mu$ (Fig. 7).
 —(ii) abundant stenoteles, capsule 7×7 - $7 \times 9 \mu$, similar to those in hydranth.
 —(iii) abundant very large heterotrichous anisorhizas, capsule 12×16 - $15 \times 14 \mu$, with long threads, concentrated in proximal parts of radial canals and tentacle knobs (Fig. 8).

Colour in life: stems greenish brown with dark brown perisarc on lower stem and hydrorhiza, coenosarc flesh pink. Tentacles translucent white, body of hydranth mushroom pink, blastostyles white, maturing gonophores orange brown. At release, jelly of medusae transparent, radial canals and tentacle knobs white with a shade of purple, reproductive products orange. Spadix of spent gonophore dark orange brown.

Remarks on the hydroid generation: *Ralpharia magnifica* possesses the largest solitary hydranth known from Australian waters and rivals in size *T. regalis* Boeck, 1860 from the northern hemisphere. This similarity is of interest, since *T. regalis* is also reported to be associated with a coralline substrate, *Lophophelia* sp., in shallow water (Broch, 1916). *R. magnifica* is a widely, although sparsely distributed species, recorded by the author from near Sydney, New South Wales, to the eastern Great Australian Bight. It invariably occurs in association with *P. membranaceum* in cool temperate waters, but may, however, be associated with other species of alcyonaria elsewhere. Because of the obligate nature of its association with *P. membranaceum*, *R. magnifica* is restricted, in Victoria, to shallow coastal reefs where the alcyonacean is abundant.

Although not truly solitary, since they are interconnected by the hydrorhiza, the stems are always well separated to allow full expansion and movement of the large hydranths. Individual hydranths are capable of considerable axial movement around the stem and are also capable of orientation in various directions independent of the current flow. This flexibility is permitted by the thinning of the perisarc in the distal stem region. Most of the colonies appear to be quite old and the majority of stems show evidence of repeated breakage, possibly due to fish grazing, followed by regeneration of the hydranths. The hydranths are evidently voracious predators, since the stomach contents often contain small crustacea; on one occasion, a small fish about 1 cm long was observed being swallowed.

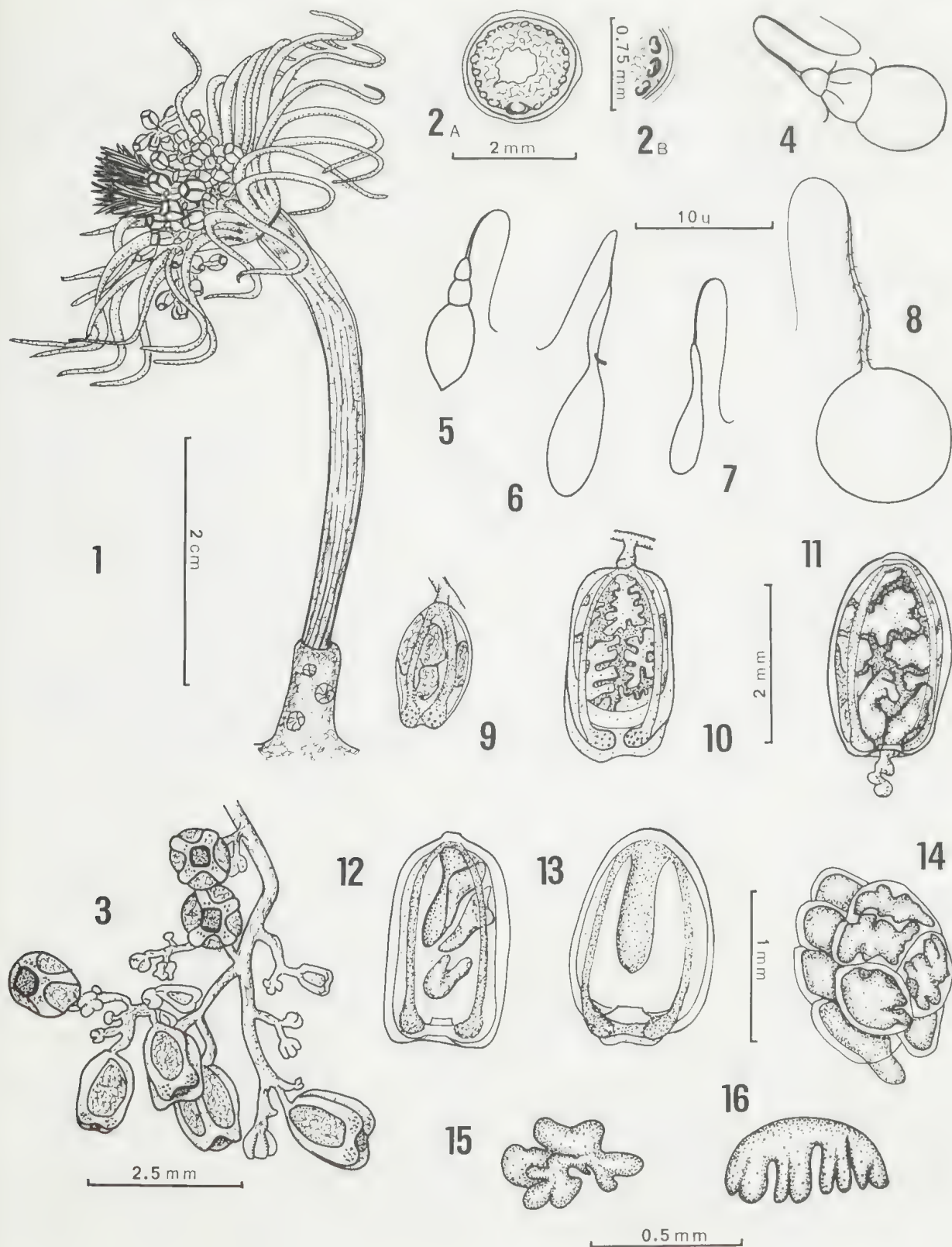
Reproduction and Development: The following

account of the reproduction and development of *R. magnifica* is from observations made in the field and from specimens reared and kept under observation in the laboratory in aerated Western Port sea water at ambient field temperature. The preserved specimens are included in the type series.

Blastostyles appear in early November and reproduction commences in early January when water temperature rises to a maximum of 20-21°C. (Western Port). Near maturity, the gonophores pulse spasmodically while still attached to the blastostyle. At this stage, both male and female reproductive products completely surround the spadices and fill the cavity of the gonophore. The 12-18 eggs are large, about 0.3 mm long, irregularly and deeply lobed, and each is enclosed in a thin transparent pellicle which attaches it to the spadix. (Fig. 14).

Medusae are synchronously liberated in large numbers at night and swim with strong jerking movements for several hours. During this time the sperm is shed rapidly from the male and the eggs are expelled one by one from the female. Although the point was not positively established, it is likely that fertilisation occurs in the water. During their expulsion from the medusa the eggs change from their original deeply lobed form and assume a lumpy amoeboid shape (Figs 11, 15). Such a high degree of plasticity would be advantageous to allow escape of the egg undamaged through the narrow orifice in the velum.

Figures 1-16. *Ralpharia magnifica* g. et sp. nov. Fig. 1. Fertile hydranth, holotype colony, drawn from underwater photograph. Fig. 2A. Transverse section through mid-stem region showing longitudinal circumferential canals. Fig. 2B. Canals, enlarged. Fig. 3. Blastostyle with gonophores in various stages of development, drawn from underwater photograph. Figs 4-8. Nematocysts (all drawn to same scale). Figs 4-5. Stenoteles from hydranth; Fig. 6. Isorhiza from hydranth; Fig. 7. ? Isorhiza from gonophore. Fig. 8. Anisorhiza from gonophore. Figs. 9-13. Stages in development of the female gonophore (all drawings to same scale from living material); Fig. 9. Immature gonophore. Fig. 10. Nearly mature gonophore with segmented ova; Fig. 11. Free medusa liberating ova. Fig. 12. Later stage, showing nearly spent medusa with few remaining ova. Fig. 13. Empty medusa showing spadix. Fig. 14. Mature ova dissected out from gonophore, showing thin pellicle covering ova (preserved material). Figs. 15-16. metamorphosis of the egg; Fig. 16. Larva 1-2 hours after expulsion, showing beginning of development of tentacles.



During the first one or two hours after expulsion, the fertilised egg contracts and arches a little in the centre; at the same time the rather shapeless amoeboid lobes become re-organised into a number of elongate processes fringing the central convexity (Fig. 16). About 20 hours after fertilisation, the central part of the larva is now a more or less circular disk and the processes have become re-arranged into 2 circlets of stubby, rudimentary tentacles (Fig. 17). At 24 hours after fertilisation, the body is top-shaped and the tentacles are more elongated (Fig. 18). After 48 hours, the larvae have 6-12 tentacles which now react to stimuli. Between 2 and 4 days after fertilisation, the tentacles reach maximum length and are now long and slender, radiating stiffly alternately upward and downward from the body (Fig. 19). The aboral pole is dome-shaped, with a conspicuous central pale pink ring.

Although the tentacles react sharply to stimuli, extended observation of 30 actinulae failed to reveal any evidence of crawling movements, it therefore seems likely that the stiffly extended tentacles may provide a passive but effective means of wide dispersal by "cart-wheeling" along with water currents.

Laboratory reared actinulae from 3-5 days old settled rapidly when placed in contact with pieces of *P. membranaceum*. Immediately on contact with the alcyonacean the actinulae orients itself in a squatting position, strongly contracting the tentacles to bring the aboral pole into contact with the substrate (Fig. 20). Within 12 hours of settlement, a short pedicel has penetrated the alcyonacean and the tentacles have resumed their normal position (Fig. 21). During the next 2 days, the tentacles contract to mere stumps while the pedicel and the hydrorhiza grow rapidly (Fig. 22). (In laboratory specimens, the maximum length attained by the pedicel and hydrorhiza was 3.5 mm). The manner by which the hydrorhiza penetrates the hard mass of the alcyonacean was not investigated, but an aureole of dead tissue at the site of penetration of the pedicel suggests that some chemical reaction takes place.

From 2-3 days after settlement, the oral pole commences to evaginate while the aboral ten-

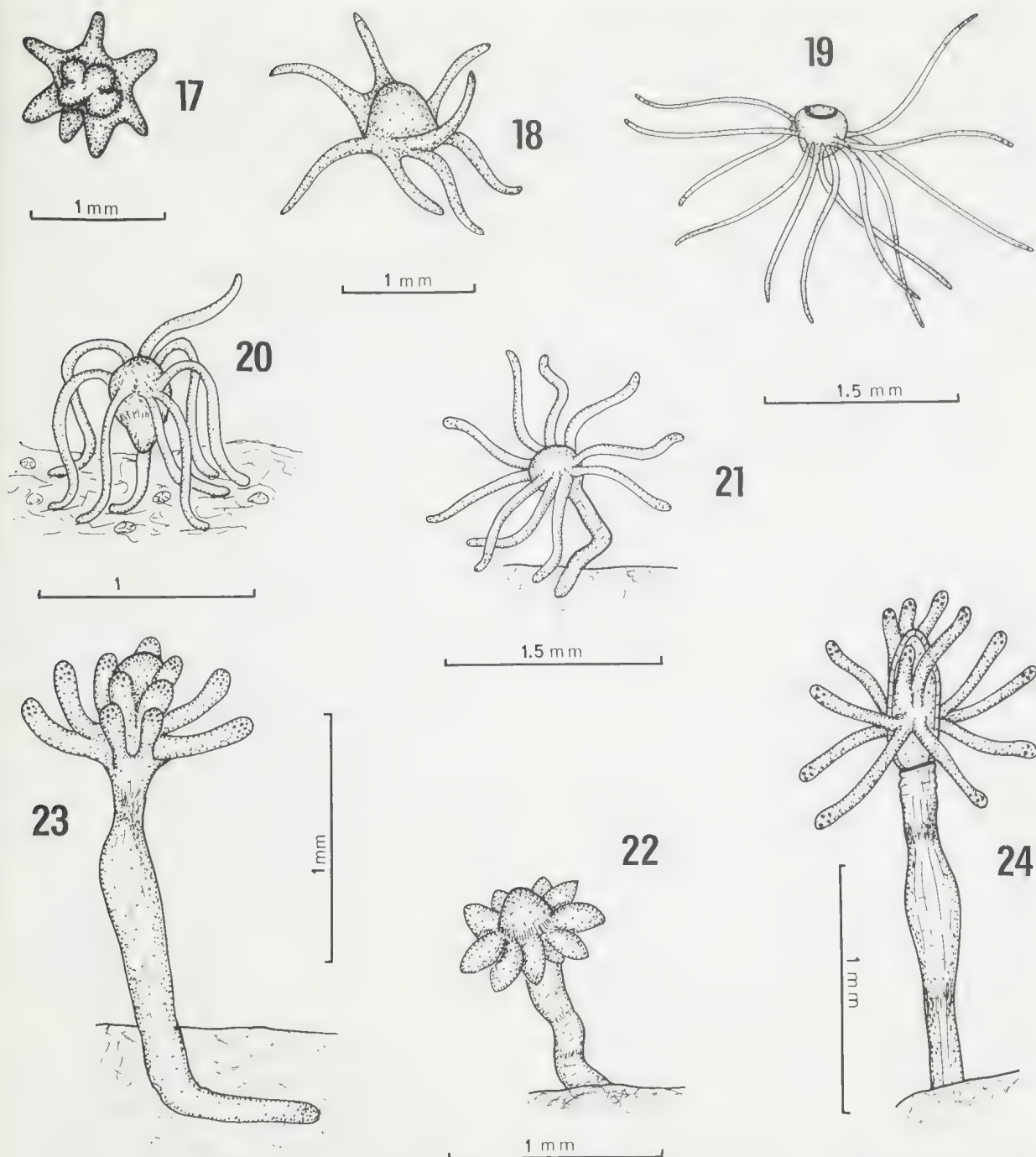
tacles of the young hydranth begin to lengthen once more. The tentacles are now thick, with blunt tips set with large nematocysts. At 4 days after settlement the oral pole has elongated to form the hydranth body. At this stage 4 oral tentacles begin to differentiate by outward and upward growth from the oral evagination. (Fig. 23). After 5 days, the body of the hydranth is clearly separated from the pedicel by a constriction identical to that seen in the mature hydranth, and during the next several days (up to 8 days after settlement) the 4 oral tentacles continue to grow. Both oral and oboral tentacles are blunt-tipped with nematocysts along most of their length, with the greatest concentrations at the tips.

At this stage the developing gastral cavity is clearly visible through the body wall and the site of the hypostome becomes visible as an apical thinning of the endoderm. (Fig. 24). A brisk internal circulation is visible in the distal region of the pedicel and in the lower gastral cavity. At this stage longitudinal striae, comprising rows of orange coloured cells, begin to form in the endoderm of the pedicel.

Because of the advancing decay of the alcyonacean substrate, the observations were terminated at this stage before the actual development of the mouth was observed and it is possible that the later stages of development of the hydranths may have become more protracted than would occur under natural conditions.

Remarks on the genus Ralpharia: There are no structures of the sterile hydranth which distinguish *Ralpharia* from other genera of the Tubulariidae. Both *Ectopleura* Agassiz, 1862, and *Hybocodon* Agassiz, 1862, have firm perisarc covered stems and liberate medusae. The medusa of *Ectopleura* has eight nematocyst tracks on the exumbrella, and may have rudimentary tentacles, while the medusa of *Hybocodon* is asymmetrical, has one long tentacle and five nematocyst tracks. Both medusae have mouths. The medusa of *Ralpharia*, because of its brief free-swimming existence, has no mouth.

Some of the features observed in the development of *Ralpharia* from ovum to young hydranth, are, according to Rees (1957),



Figures 17-24. Stages in development of the actinula and young hydranth of *Ralpharia magnifica* g. et sp. nov. Fig. 17. Actinula with rudimentary tentacles, 20 hours after release from medusa. Fig. 18. Commencement of elongation of tentacles, 24 hours after release. Fig. 19. Actinula 2-4 days old, with fully developed tentacles. Fig. 20. Actinulae settling on to alcyonacean substrate. Figs. 21-24. Development of young hydranth. Fig. 21. Hydranth 12

hours after settlement, section of alcyonacean cut away to show penetration of hydrorhiza. Fig. 22. Contraction of tentacles, further development of pedicel and hydrorhiza 2 days after settlement. Fig. 23. Evagination of oral pole and commencement of differentiation of oral tentacles 4 days after settlement. Cut away section showing further development of hydrorhiza. Fig. 24. Young hydranth with growing oral tentacles and developing gastral cavity.

characteristic of the more primitive Athecata. Rees considers that the Corymorphidae are ancestral to the Tubulariidae because of the presence of an elastic pellicle surrounding the fertilized amoeboid egg in *Corymorpha nutans* Sars, 1835, and in *C. palma* Torrey, 1907 (Rees, 1937). Torrey (1907) notes that the larva of *C. palma* is mobile before settling. The eggs of *Hybocodon prolifer* Agassiz, 1862, are also amoeboid in shape and are brooded in the medusa until development of the actinula (Russell, 1953). There is little information on the development of the egg of *Ectopleura*. The expulsion of the egg of *R. magnifica* while still in the amoeboid stage and covered by a protective pellicle is evidence of a close relationship with the Corymorphidae and provides an evolutionary link between the Corymorphines and the more advanced Tubulariidae. Rees (1957) also noted that the pellicle surrounding the egg of *Corymorpha nutans* was pushed out into pseudopodia-like processes and then atrophied to form the anchoring filaments of the young hydranth. He also remarked that Manton's (1940) observations of the shrinkage of the larval tentacles of *Myriothele phrygia* (Fabricius), exposing the central disk, is evidence of the primitive relationship between the Corymorphidae and the Myriotheleidae. The slow development of the pseudopodia-like lobes of the larva of *R. magnifica* into the tentacles of the actinula, and later, partial resorption of the tentacles in the post-settling phase thus provides evidence for the relationship of *R. magnifica* with the more primitive members of the Capitata.

The lengthy actinula stage and the late development of the oral tentacles and mouth of the young hydranth are without parallel in the literature of the Tubulariidae. *T. larynx* and its congeners, which have received most study, are essentially estuarine species. Adaptation to the restricted but rigorous estuarine environment would demand brooding of the larva to an advanced stage followed by rapid settling and metamorphosis. In contrast, a relatively long planktonic actinula stage would favour dispersal of oceanic species, particularly substrate specific forms such as *R. magnifica*, and no adaptive advantage would be gained by a

mobile actinula. The delayed development of the oral tentacles and mouth until after the young hydranth is rooted and the pedicel is long enough to hold the hydranth clear of the substratum again lies in environmental demands since rapid establishment of a secure hydrorhiza would be imperative in a regime of strong water movement.

***Tubularia ralphi* Bale, 1884**

Tubularia ralphi Bale, 1884, p. 42; Hickson & Gravely, 1907, p. 13; Broch, 1948, p. 6.

Tubularia gracilis Von Lendenfeld, 1885, p. 597.

Tubularia australis Stechow, 1924, p. 5; 1925, p. 196.

Tubularia warreni Ewer, 1953; Millard 1975, p. 35.

Tubularia larynx Ellis & Solander, 1786; Fenchel, 1905; Ralph, 1966, p. 158.

?*Tubularia crocea* (Agassiz, 1862); Pennycuik, 1959, p. 157.

Tubularia marina Torrey, 1902; Russ & Wake, 1975, p. 9.

Material: The following description is from the neotype, NMV G3227. Colony preserved in 5% formalin. Coll: Yarra River Entrance Beacon, Port Phillip, Victoria, 3/4/77, 1-2 m deep, on mussels, *Mytilus edulis* Lamarck, and on the ascidian *Styela clava* Herdman.

Other records: Inkerman Creek, Queensland, J. E. Watson 20/5/77; Port Kembla Harbour, New South Wales, J. E. Watson, 6/2/77; Popes Eye Reef, Port Phillip, J. E. Watson, 14/6/79.

Description: Colonies growing in hand-sized tufts to 12 cm high, comprising up to several hundred individual stems. Hydrorhiza a matted reticulum of tubes of the same diameter as stems. Individual stems range up to 12 cm but averaging 6-8 cm long, simple, tubular, 0.3-0.5 mm diameter, occasionally branched, each bearing a terminal hydranth. Perisarc of stems smooth with groups of 3-8 annulations at intervals, becoming thinner distally. Coenosarc of stem divided into 2 longitudinal canals which

terminate in indistinct striae below the hydranth. (Fig. 26).

Mature hydranth variable in size, ranging up to 15 mm in diameter across the extended aboral tentacles in living specimens. Aboral tentacles in 1 verticil, 4-5 mm long, tapering, the number varying from 16-27 according to age of the hydranth. Oral tentacles 2-3 mm long, usually 15-25 in a single verticil, but always less than the number of aboral tentacles, with blunt tips.

Blastostyles arising just above aboral tentacles, usually a maximum of 12 with 6-8 in a more advanced state of development than the others. Mature blastostyles branched, longer than the oral tentacles, pendulous, bearing clusters of up to 46 gonophores in various stages of maturity. Male and female gonophores borne on short pedicels on different hydranths, mature gonophores oval to spherical, about 0.3 mm in diameter. Female gonophore containing 6-8 ova (in lower latitudes there are 2-4 ova) 2-3 of which develop into actinulae. Spadix of immature female gonophore large, tapering distally, later displaced to one side by growing actinulae. Gonophore surmounted by 8 transparent radial crests and a long, central protrusion of the spadix. At maturity the crests may be resorbed to mere knobs and the spadix is replaced by a tentacle of the most advanced actinula. Immature male gonophore elongate oval, becoming spherical near maturity. Mature gonophore with central spadix and usually without apical processes. (Fig. 28). There is, however, considerable variability throughout the colony, and even on the one hydranth. Variations include a bun-shaped apical process, often associated with an almost spherical gonophore (Fig. 29), a short protrusion of the spadix which may be accompanied by 4 incipient apical crests, or 4 raised knob-like processes. (Fig. 30).

At liberation the actinula has 8 aboral tentacles with swollen tips and 5-8 rudimentary oral tentacles. It performs sluggish swimming and crawling movements prior to settling. Settling occurs within 24 hours by attachment of the aboral pole, followed by rapid elongation to form a stem and development of the capitate oral tentacles. After 36 hours the young

hydranth has a well developed hypostome and a short, annulated stem.

Nematocysts of four kinds present:

Heterotrichous anisorhizas—capsule spherical, 7-9 μ diameter, thread very long, abundant on male gonophores, rare on hydranth and female gonophores. (Fig. 33).

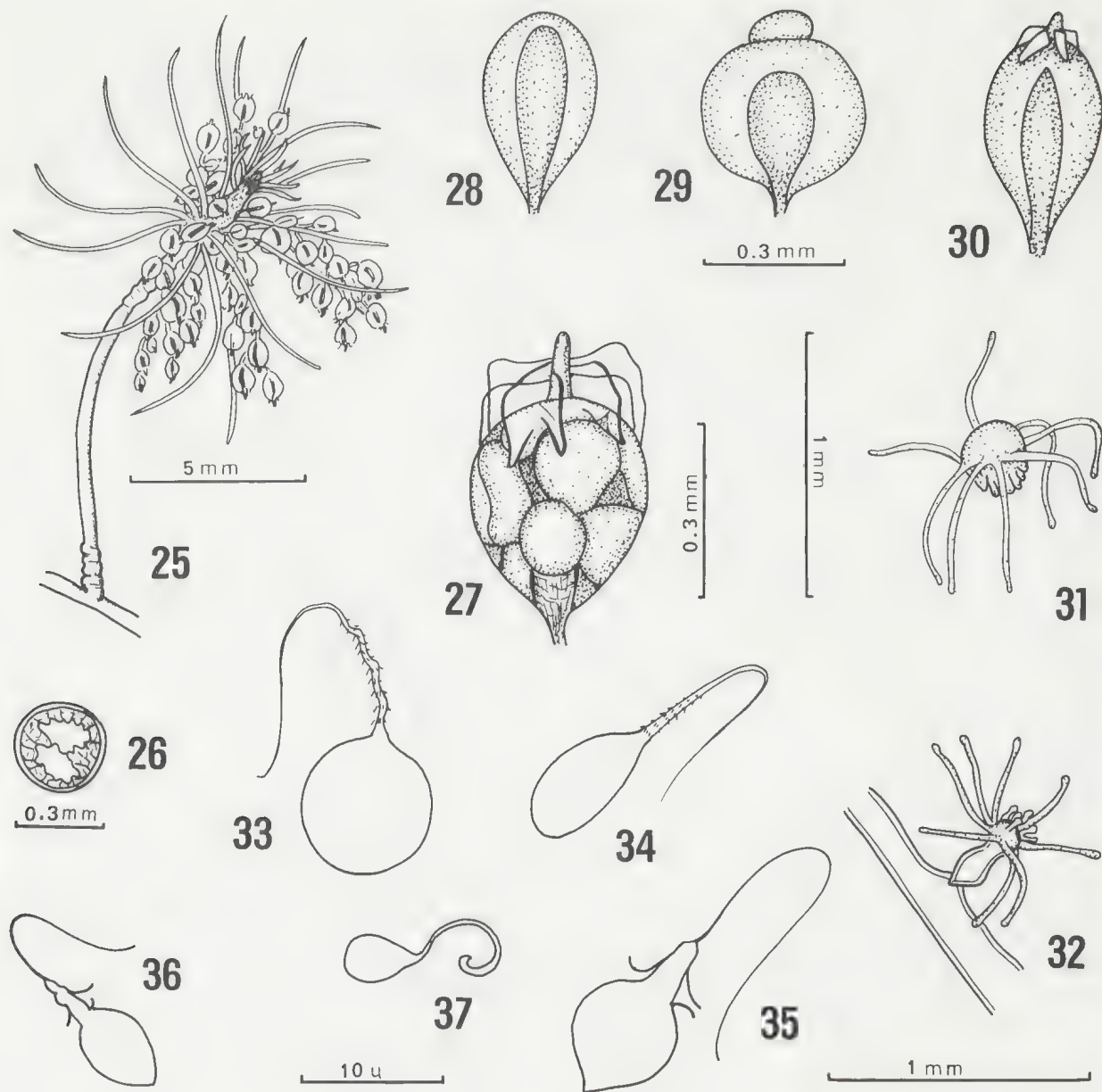
Basitrichous isorhizas— $7 \times 4 - 9 \times 4 \mu$, very abundant on hydranth and female gonophores. (Fig. 34).

Stenoteles— (i) Large, almost spherical, 6-8 μ diameter, very abundant on male gonophore. (Fig. 35). (ii) Smaller, oval, $5 \times 4 - 6 \times 5 \mu$, butt 3 μ long, very abundant on hydranth, rare on gonophores. (Fig. 36).

Desmonemes—small, $4 \times 3 - 6 \times 4 \mu$, with 4 coils, abundant on hydranth. (Fig. 37).

Colour: Stems pale straw colour, body of hydranth and spadix usually orange red and tentacles transparent white. Variations are common, including golden, brown, or pale green hydranths and gonophores. The ova are always creamy white.

Remarks: Branching among the colonies is due to the settling of actinulae on adjacent stems of the parent colony, the annulated stem of the young hydranth forming the base of the new branch. There is a tendency for all hydranths on the one colony to be the same sex; however, both male and female may occur on the one colony. Both the hydranth and blastostyles are very active, the pendulous blastostyles performing rhythmic lashing movements at intervals. Although its preferred substrate is mussels, *T. ralphii* grows on solitary ascidians, on other animal substrate and on ropes, metal and wooden structures. The most luxuriant colonies occur in the upper water column in estuarine situations such as Hobsons Bay where salinity may vary from 9‰–35‰. *T. ralphii* also occurs in fully marine waters, but the colonies tend to luxuriant growth only in good current flow and in reduced light. *T. ralphii* is an important member of the summer fouling community of Hobsons Bay where it grows rapidly and reproduces after the summer temperature peak of 21°C.



Figures 25-37. *Tubularia ralphii*.

Fig. 25. Mature female hydranth with gonophores, drawn from underwater photograph. Fig. 26. Transverse section through mid-stem region showing 2 longitudinal canals. Fig. 27. Nearly mature female gonophore with transparent apical crests and protruding spadix. Figs 28-30. Morphological variations of nearly mature male gonophore (all drawn to same scale). Fig. 28. Most commonly occurring gonophore without apical processes. Fig. 29. Gonophore

with bun-shaped apical process. Fig. 30. Gonophore with incipient lateral crests. Fig. 31. Newly liberated actinula. Fig. 32. Young hydranth 24-36 hours after settlement. Figs 33-37. Nematocysts (all drawn to same scale). Fig. 33. Heterotrichous anisorhiza from male gonophore. Fig. 34. Basitrichous isorhiza from female gonophore. Fig. 35. Stenotele from male gonophore. Fig. 36. Stenotele from hydranth. Fig. 37. Desmoneme from hydranth.

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TAXONOMIC REVISION OF THE ELAPID SNAKE GENUS *DRYSDALIA* WORRELL 1961

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Abstract

The southern Australian snake genus *Drysdalia* (Worrell 1961) is reviewed and a key provided for the four species recognised. *Drysdalia rhodogaster* (Jan 1963) is elevated from synonymy and fully described for the first time. The types of each species are discussed in detail and lectotypes nominated where necessary.

Introduction

Boulenger (1896) allocated many of the small Australian elapid snakes to the genus *Denisonia* Krefft, 1869. Australian herpetologists followed Boulenger's scheme until the genus *Denisonia* became an unwieldy, polyphyletic taxon. For example, Kinghorn (1956) listed 19 (27.5%) of the 69 Australian elapid species and subspecies under this genus. In 1961 Worrell revised the genus *Denisonia* and re-allocated the previously included species to ten genera, eight of which he described for the first time. Worrell's revision proved controversial and some of his allocations were not accepted. Cogger (1979) presents a consensus view of the accepted taxa.

The genus *Drysdalia* was erected by Worrell in 1961 to receive three species (*Elaps coronatus* Schlegel, 1837; *Hoplocephalus coronoides* Günther, 1858; and *Hoplocephalus mastersii* Krefft, 1866) which Boulenger (1896) had placed in *Denisonia*. *Drysdalia* has been widely accepted as a valid genus but it has become apparent that the included species are in need of revision. The present revision has involved examination of all specimens held in the National Museum of Victoria, the Western Australian Museum, the South Australian Museum and the Australian Museum. In addition, all relevant type specimens for species now included in *Drysdalia* have been examined. As a result of this revision four species are now recognized, each occupying a discrete geographical range:

Drysdalia coronoides (Günther, 1858)

South-eastern Australia, Bass Strait Islands and Tasmania.

Drysdalia coronata (Schlegel, 1837)

South-western Australia and associated islands.

Drysdalia mastersii (Krefft, 1866)

Southern South Australia and adjacent areas in Western Australia and Victoria.

Drysdalia rhodogaster (Jan, 1863)

South-eastern New South Wales.

As there is an extensive literature on venomous snakes, mainly for the popular market, only publications considered to be of primary taxonomic importance have been included in the synonymies.

Abbreviations used for institutions in this paper are:

Australian Museum	AM
British Museum (Natural History)	BM(NH)
Muséum National d'Histoire Naturelle	MNHP
National Museum of Victoria	NMV
South Australian Museum	SAM
Western Australian Museum	WAM

Key to species of *Drysdalia*

1. Distinct white stripe edged above by black running along upper labials from below the nostril, under the eye often to the neck 2.
Lacking distinct white stripe running along upper labials *D. rhodogaster*
2. Distinct pale or dark band (sometimes broken medially) across the nape 3.
Lacking band across the nape
. *D. coronoides*
3. *Band across the nape black . *D. coronata*
Band across the nape pale yellow-orange *D. mastersii*

* Some specimens from the Archipelago of the Recherche lack the black band across the nape. *D. coronata* can usually also be distinguished from other species of the genus by its broader frontal. See Table 1.

Drysdalia Worrell, 1961

- Elaps* (part) Schlegel, 1837, *Partie Générale*: 180-182, *Partie Descriptive*: 435-444.
Alecto (part) Duméril and Bibron, 1854: 1249.
Alecto (part) Jan, 1863: 116-117.
 (part) Jan & Sordelli, 1873: pl. 1, figs. 1 & 3, pl. 2, fig. 2.
Hoplocephalus (part) Günther, 1858: 213.
 (part) Krefft, 1869: 53.
Denisonia (part) Boulenger, 1896: 333.
 (part) Waite, 1929: 217.
Drysdalia Worrell, 1961: 25 (type species *Hoplocephalus coronoides* Günther, 1858 by original designation).
 Worrell, 1963: 122-123.
 Cogger, 1975: 382-383.

Diagnosis: Small, rather slender snakes ranging from a minimum total length of 100 mm (snout-vent length 80 mm) to a maximum total length of 650 mm (snout-vent length 550 mm). Nostril in single nasal. Frontal longer than broad, less than one and a half times width of supraocular. Internasals present. Suboculars absent. Dorsal scales smooth, 15 scale rows at midbody, very rarely 17. Lower lateral scales not noticeably enlarged. Ventral scales smooth and unkeeled, range from 123 to 157. Subcaudal scales smooth and undivided, range from 32 to 67. Anal scale undivided. Posterior process of maxillary bone short, 3 to 5 solid maxillary teeth follow the hollow fang.

***Drysdalia coronata* (Schlegel, 1837)**
 Crowned Snake

- Elaps coronatus* Schlegel, 1837, *Partie Générale*: 182, *Partie Descriptive*: 454. Type locality: Nouvelle Hollande (= Australia).
 Gray, 1841: pl. 5, fig. 2.
 Guibé & Roux-Estève, 1972: 133.
Frimesurus olivaceus Gray, 1841: 443. Type locality: New Holland.
Elaps melanocephalus Gray & Neill, 1845 (non Wagler, 1824): 416.
 Type locality: King Georges Sound.
Alecto coronata Duméril & Bibron, 1854: 1255, pl. 76, b, fig. 2.
Hoplocephalus coronatus Günther, 1858: 215.
 Krefft, 1869: 62, pl. 6, fig. 3.
Denisonia coronata Boulenger, 1896: 335.
 Waite, 1898: 55.
 Glauert, 1950: 40.

Denisonia coronoides Glauert, 1950: 41.

Drysdalia coronata Worrell, 1961: 25.

Worrell, 1963: 122.

Cogger, 1975: 382.

Types: Schlegel (1837) wrote his "Essai sur la Physionomie des Serpens" in two sections. The first section of 251 pages entitled "Partie Générale" was a general account of snakes, while the second section of 606 pages entitled "Partie Descriptive" was a more detailed account of the species and genera. *E. coronatus* was described in both sections (see synonymy) and Sherbourne (1925) lists both of these descriptions as parts of the original. The description on page 182 of "Partie Générale" provided ventral and subcaudal counts for a single specimen, while that on pages 454-455 of "Partie Descriptive" has ventral and subcaudal counts, plus snout-vent and tail length measurements for two specimens. The scale counts provided on page 182 differed from those provided on page 455, thus it would appear that Schlegel had at least three specimens which he referred to *Elaps coronatus* in 1837. The existence of the first part of the description was apparently last noted by Gray (1841) until Guibé and Roux-Estève (1972), as major works between these times have listed the second part of the description as the original. Consequently this has led to the belief that *E. coronatus* was based on two syntypes. Guibé and Roux-Estève (1972) listed two specimens in the *Muséum National d'Histoire Naturelle*, Paris as syntypes.

All the specimens examined by Schlegel in 1837 were collected from "Nouvelle Hollande" (= Australia) by Quoy and Gaimard or by Péron and Lesueur. Schlegel (1844) gave the distribution of the species as south western Australia. Duméril and Bibron (1854) recorded that two of Schlegel's specimens were collected from "Port du Roi Georges de la Nouvelle Hollande" (= King Georges Sound) by Quoy and Gaimard.

Four possible type specimens were located in the *Muséum National d'Histoire Naturelle*, Paris in 1973. Two of these are not indicated as types in the catalogues and are registered simply as having been collected from "Australia" by Quoy and Gaimard (MNHP No. 4694) and Péron (MNHP No. 4695). There is no indica-

tion in the catalogues that these were Schlegel types, and Guibé and Roux-Estève (1972) did not consider that they belonged to the type series. The remaining two specimens (MNHP No. 321—old number 4696, and MNHP No. 7677—old number 4697) are both indicated as Schlegel types in the catalogues and both are registered as having been collected from "Port du Roi Georges" by Quoy and Gaimard. These are the two specimens listed by Guibé and Roux-Estève as syntypes. One of these specimens (MNHP No. 7677) now has a damaged tail and cannot be compared to the original description. The second specimen (MNHP No. 321) is complete and agrees in scalation and dimensions with one of Schlegel's types. This specimen is selected as lectotype.

Lectotype: MNHP No. 321 (old number 4696). Muséum National d'Histoire Naturelle, Paris.

Locality: Port du Roi Georges de la Nouvelle Hollande (=King Georges Sound, Western Australia), Quoy and Gaimard.

Description: Snout-vent length 250 mm. Tail length 59 mm. Total length 309 mm. Scales round midbody 15. Ventral scales 143 (Schlegel, 1837, 142; Guibé and Roux-Estève, 1972, 138—see below*). Subcaudals undivided, 51 (Schlegel 54, Guibé & Roux-Estève, 48). Anal scale undivided. Upper labials, 6, 3rd and 4th subocular. Lower labials 7. Internasals one third the size of the pre-frontals. Temporals 2+2.

Colour: Dorsal surface brown. Ventral surface light brown. Distinct black stripe bordered below by white runs across the nape then forward along the upper lip below eye and around snout.

Condition: Well preserved.

Paralectotype: MNHP No. 7677 (old number 4697), Muséum National d'Histoire Naturelle, Paris. Data as for lectotype. Ventral scale count 141. Subcaudal scales undivided, tail truncated. Lower labials 6. All other details as for lectotype.

The paralectotype and other two specimens possibly available to Schlegel are conspecific with the lectotype.

Trimesurus olivaceus Gray 1841, was included in the synonymy of *Denisonia coronata* by Boulenger (1896) although Gray did not mention the species in publications subsequent to the original description. Boulenger's action is followed as Gray's (1841) description fits *D. coronata* as recognized here. No type specimen has been located. Gray did not list a type specimen, or possible type specimen in his British Museum Catalogue (1849) and neither did Günther or Boulenger in their catalogues published in 1857 and 1896 respectively. As searches of collections in most of the major European Museums were made in 1973-74, the type is presumed lost.

Elaps melanocephalus Gray and Neill 1845, has not subsequently been mentioned in the primary taxonomic literature (e.g. Boulenger 1896). We consider Gray and Neill's description to be inadequate, and tentatively include the name in the synonymy of *D. coronata* as the type locality given was King Georges Sound. No type specimen has been located and, as with *T. olivaceus*, no mention is made of a type or possible type in any of the British Museum catalogues. For these reasons, as with *T. olivaceus*, the type is presumed lost.

As Wagler (1824) used the combination *Elaps melanocephalus*, Gray and Neill's (1845) name is a secondary homonym.

Other Specimens Examined

A further 158 specimens were examined—147 from the mainland and 11 from the Archipelago of the Recherche. From these is derived the following general description.

Size: Largest adult: Snout-vent length 548mm; tail length 103mm; total length 651mm.

* Peters, 1964: 378 lists three methods employed to make ventral scale counts. Method 2 has been used throughout this paper. Guibé & Roux-Estève probably used Method 1 which gives a slightly lower count.



Figure 1—Map showing distribution of *Drysdalia coronata*.

Juveniles at birth: snout-vent length 136 mm; tail length 28 mm; total length 164 mm.

Scalation: Scales round midbody 15, (WAM R41717 had 17 anterior rows and 15 at mid-body). Ventral scales range from 132-157 with a mean of 142.7 (N=158). There was some evidence of an increase with latitude and insularity as mainland specimens ranged from 132-152 with a mean of 142.2 (N=147) and Recherche Archipelago specimens ranged from 145-157 with a mean of 150.4 (N=11). Subcaudal scales were all undivided and ranged from 36-54 with a mean of 44.3 (N=149). Once again there was some evidence of an increase with latitude and insularity as mainland specimens ranged from 36-52 with a mean of 44 (N=138) while Recherche Archipelago specimens ranged from 42-54 with a mean of 50.2 (N=11). Anal scale undivided in all specimens.

Colour: Dorsal surface light brown to dark olive brown, ventral surface lighter, yellowish to pale olive, base of ventral scales normally darker. Head normally darker than body with a distinct black stripe bordered below by white running across the nape then forward along upper lip below (and sometimes through) eye then around snout. In some specimens from the Archipelago of the Recherche the band across the nape was reduced and in two specimens (AM Nos. R7715-6) it was absent altogether.

Localities and Registered Numbers:

Western Australia. (WAM) No data R4233; Muchea R459; Jandakot R1206; Perth R1326; Bunjil R1335; Tambellup R2104; North Perth R4835; Belmont R4976, R14485; Denmark R4993-4, R10098, R24960-2, R30680; King River, near Albany R5615; Busselton R6057, R6196, R9597; Wanneroo R6346; Bornholm R6483; Cranbrook R6566; Albany R7763-4; Waroona R7813; Bokol R8370; Millbrook R8922; Esperance R8938, R11365, R13674, R17863; Wagerup R8986, R9364; Mondrain Island R10106, R53119; Armadale R13817; Mount Many Peaks, via Albany R14167; Israelite Bay R14205; Geraldton R15071; Safety Bay R15072; Cheyne Beach R15073, R31169; Dalyap River R15075; 22 km E. of Esperance R15076; Jerramungup R18547; Doubtful Island Bay R19798-9; Upper Kalga R21368-70; Witchcliffe R21965; 32 km E. of Esperance R21995; Frenchmans Bay, Albany R22483-8; Penguin R22489; Augusta R24906; 5 km N. of Cape Leeuwin R25879; Cape Le Grande R29643; ?Bunbury R31196; Rockingham R36175; Ruddocks Cave, near Witchcliffe R36716; Middle Mount Barren R36899; Boondadap River R37217; Two People Bay R37837-8, R44995; Riverton R39781; Scott River R41717; Middle Island R41915, R47725; Mississippi Bay, Cape Le Grande National Park R41955, R41959; 4 km N. of Frenchmans Peak, Cape Le Grande National Park R41957; Mount Merrivale, near Esperance R43884; West of Point Culver R44973; Bremer River R45651; Kent River Area R46544-5; Merrap R47885, R51472-3; Walpole R51472-3; Bluff Knoll R51775-6; Cranbrook or Broomhill R53735-6; Serpentine R53737; 5 km N. of Fitzgerald Inlet R55936; (AM) No data 5745; Western Australia 6604-6, R10461; King George's Sound 6601, 6603, 6607, 6611-2, 6615; Bornholm R7688; Mondrain Island R7715-6; Mississippi Bay, Cape Le Grande National Park R7717; Tambellup R9891, R11104, R11531, R13137; Esperance R30342, R74152-60; Albany R74150-1; (NMV) No data 61153; Western Australia R702, R2792-3, R11114-20, R11122-4, R12824, D6376; Champion Bay R2791; Archipelago of the Recherche D8255; Perth D8832.

Drysdalia coronoides (Günther, 1858)

White-lipped Snake

Hoplocephalus coronoides Günther, 1858: 215.

Type locality—Tasmania.

Kreffl, 1869: 62-63. pl. 12. figs. 1, 1a.

Alecto labialis Jan & Sordelli, 1873, (non Jan, 1859): pl. 1, fig. 1. Type locality—Australia.

Denisonia coronoides: Boulenger, (part) 1896: 336.

Waite, (part) 1898: 55.

Waite, (part) 1929: 220-221.

Kinghorn, 1929: 174.

Worrell, 1956: 206-7.

Denisonia nigra De Vis, 1905: 50. Type locality—Tasmania.
= *Denisonia coronoides* (Günther, 1858) after Mack & Gunn, 1953: 63.

Denisonia coronoides coronoides Kinghorn, 1956: 163.

Drysdalia coronoides Worrell, 1961: 25.

Worrell, (part) 1963: 122.

Cogger, 1975: 383.

Types: Günther (1858) listed 18 specimens in the original description but Boulenger (1896) mentioned only 16 types. Sixteen type specimens were located in the British Museum (Natural History) in 1973 and all could be traced directly to Boulenger's list (p. 337) as specimens A, a-i and k-q and to Günther's type list (pp. 215-216) excluding one specimen designated as f and the second of the two specimens designated under n. These specimens were not entered in the Museum's accessions books or registers and, as Boulenger did not list them, it is assumed they were lost prior to 1896.

In order to stabilize Günther's name *coronoides* and limit the type locality, one of the nine specimens collected in Van Diemens Land (= Tasmania) by Mr. R. Gunn has been selected as the lectotype.

Lectotype: BM(NH) 1946.1.17.39 (old number 52.1.15.29), British Museum (Natural History), London.

Locality: Van Diemens Land (= Tasmania), R. Gunn.

Catalogue References: Günther (1858) Specimen a; Boulenger (1896) specimen A. a.

Description: Snout-vent length 342 mm. Tail length 81 mm. Total length 423 mm. Scales round midbody 15. Ventral scales 150 (Boulenger, 1896, 151). Subcaudal scales un-

divided, 45. Anal scale undivided. Upper labials 6, 3rd and 4th subocular. Lower labials 6. Rostral contacts 1st labials, nasals and internasals. Single preoculars contact 2nd and 3rd labials, nasals, prefrontals and supra-oculars. Frontal contacts prefrontals, supra-oculars and parietals. Post-oculars paired, contact supra-oculars, parietals, upper anterior temporals and 4th and 5th upper labials. Temporals 2 + 2.

Colour: Dorsal surface brown, ventral surface grey speckled with black. Distinct white stripe edged above by black runs from below nostril under eye to neck.

Condition: Well preserved but epidermal scales sloughing off in parts.

Comment: This specimen has been chosen as lectotype as it agrees with the description and locality data published by Günther (1858); it was part of a series of specimens collected by R. Gunn in Tasmania; and also it was specimen 'a' in Günther's and Boulenger's catalogues which is often an indication the specimen was the original author's primary specimen. In addition the lectotype has reliable documentation, as all jar labels and entries in old and new accessions books, museum registers and published catalogues agree. The lectotype was also the best preserved of the available syntypes.

Paralectotypes: All in British Museum (Natural History) London.

Tasmania, R. Gunn, BM(NH) 1946.1.17.40; BM(NH) 1946.1.17.43; BM(NH) 1946.1.19.1-4; BM(NH) 1946.1.20.74-75: Tasmania, A. J. Smith, BM(NH) 1946.1.17.44-45: Australia, Earl of Derby, BM(NH) 1946.1.17.47: Tasmania, Zoological Society, BM(NH) 1946.1.17.49: Swan river ? BM(NH) 1946.1.20.59: Tasmania, Lords of the Admiralty BM(NH) 1946.1.20.60-61.

Ventral scale counts in order of current registration numbers are: 142, 142, 147, 143, 141, 148, 144, 144, 143, 147, 147, 144, 147, 140, 148. This gives a range of 140-150 for the type series with a mean of 144.8.

Subcaudal scale counts in order of current registration numbers are: 50, 49, 54, 54, 41, 56,

45, 49, 49, 54, 48, 46, 47, 53, 57. This gives a range of 41-57 for the type series with a mean of 49.8.

Coloration of paralectotypes as for lectotype. All paralectotypes are conspecific with the lectotype.

Alecto labialis Jan and Sordelli 1873, is a primary homonym of *Alecto labialis*, Jan 1859. The specimen illustrated by Jan and Sordelli from the "Musée de Paris" is obviously referable to *D. coronoides* as recognized here and a series of specimens registered in the MNHP as *Alecto labialis*, Jan, (MNHP Nos. 4694 (1-10), 4695 and 4695(a)) are all conspecific with the lectotype of *D. coronoides*.

Denisonia nigra De Vis 1905, described from a specimen from Tasmania was relegated to the synonymy of *D. coronoides* by Mack and Gunn (1953). The holotype in the Queensland Museum (Reg. No. QM J196) is conspecific with the lectotype of *D. coronoides*.

Other Specimens Examined

In order to determine the intraspecific variation in some important taxonomic characters a further 294 specimens were examined—210 from the Australian mainland and 84 from Bass Strait and Tasmania.

Size: Largest adult: Snout-vent length 400 mm; tail length 103 mm; total length 503 mm. Juveniles at birth: Snout-vent length 99 mm; tail length 27 mm; total length 126 mm.

Scalation: Scales round midbody 15 in all specimens except NMV D35781 from Deal Island, Bass Strait which has 17. Ventral scales range from 123-152 with a mean of 138.4 (N=294). There was some evidence of an increase with latitude as mainland specimens ranged from 123-149 with a mean of 137.3 (N=210) while Bass Strait and Tasmanian specimens ranged from 128-152 with a mean of 141.7 (N=84). Subcaudal scales were all undivided and ranged from 38-67 with a mean of 47.3 (N=276). Once again there was some evidence of an increase with latitude as mainland specimens ranged from 38-67 with a mean of 46.4 (N=204) while Bass Strait and Tasmanian specimens ranged from 41-64 with a

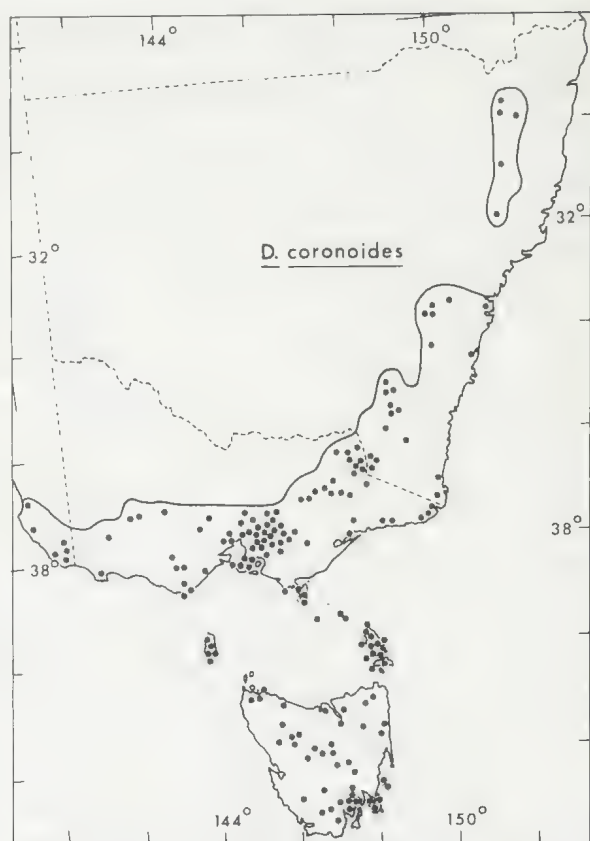


Figure 2—Map showing distribution of *Drysdalia coronoides*.

mean of 49.7 (N=72). Anal scale undivided in all specimens.

Colour: Juveniles at birth: Dorsal surface black, ventral surface salmon pink to orange. Head same colour as body with a white stripe edged above by black running along the upper lip from the nostril under the eye to the neck and sometimes beyond. Adults: Brown or olive green dorsal surface, ventral surface salmon pink to orange often merging into light green anteriorly. Head same colour as body with a white stripe edged above by black running along the upper lip from the nostril under the eye to the neck and sometimes beyond. In Tasmania the duller colours prevail and sometimes there is a second white stripe running from the upper temporal area to the neck.

Localities and Registered Numbers:

South Australia. (SAM) Lake St. Clair, near Robe R341; Port McDonnell R3714; Kingston R13403; Cape Banks R14722; (NMV) Mt. Gambier D35746-9; D35751-2; 16 km N. of Mt. Gambier D35755-8.

New South Wales. (AM) Walcha R1503; North Shore, Sydney R1605; Cooma R3362; ? Narromine R3607-8; Mt. Kosciuszko R5108, R6508, R9451, R10533, R13022, R58529-33; Ben Lomond R6776; Wee Jasper R7122; Glenlea, Glen Innes district R9388, R59242; Pambula R12605; Tubrabucca R13350-1; Goodradigbee Caves R25985; Mt. Kaputar National Park R26170; Shellharbour R27459; 7.2 km N. of Taralga R29737; Nadgee Nature Reserve R41651; 8 km W. of Jenolan Caves R58535; 8 km S.W. of Guy Fawkes R58540; (NMV) Kian-dra D35710-11; Mt. Kosciuszko D35715-6, D35723-4, D35778-80; 16 km N. of Tin Mine Huts D35727-8; Dead Horse Gap D35741; Mt. Victoria D37808; 9 km S. of Tarana D39509; 12 km W. of Jenolan Caves D39510. Locality for (AM) R3607-8 is presumed to be in error following the entry in the Australian Museum register.

Australian Capital Territory. (AM) Uriarra R2497; Brindabella Ranges R25985; (NMV) Piccadilly Circus D35714; Mt. Franklin D39219.

Victoria. (SAM) Maroondah Dam R3935; (AM) Portland R11749; Altona R13897; 3.2 km W. of Weeragua R58534; 4.8 km W. of Mt. Hotham R58536; 8 km W. of Mt. Hotham R58537; Mt. Hotham R58538; 24 km N. of Benambra R58539; (NMV) Yarra River 42981-2; Croydon R2901-2, R11038, R11043; Gembrook R8048, R8117; Beaconsfield R10865; Upper Yarra R11025; Western Port R11026, D4439; Gippsland R11027, D3606; Ringwood R11028, R13597-8, D3597-8; Wilsons Promontory R11029; Murray River R11032; Bruthen R11044; Darby River R11047, D35775; Laverton R13599, D35759; Wannon D2720; Bungaree D4267; Frankston D4334; Belgrave D4584-5; Pt. Nepean D4611; Orbost D4665; Wandin D5555; Mt. St. Leonard D7863; Selby D7994; Blanket Bay D8072; Kinglake D8759; The Basin D8852, D35732-3, D35763; Ferny Creek D8965; Glengarry

D10043; Shelley D17181, D17212, D18006, D18152; Paynesville D17765, D35731; Pom-borneit East D18239; Mt. Hotham D18269; Anglesea D33167-8; Grampian Ranges D33167; Cape Otway D33390, D35726; 1.6 km N.W. of Mt. Buangor D33494; Junction of Latrobe River and Hawthorn Creek D33606; Burney D33656; Mt. Disappointment D34162, D35734-6, D35739-40, D37821-6, D37828; Red River Inlet D34249-50; Tidal River D35708; Point Cook D35709; Martins Hill D35717; Penny-saddle D35718; Mt. Baw Baw D35721-2; 16 km W. of Cowombat Plains D35725; Murrindindi D35745; Pirron Yallock D35753; 3.2 km W. of Frankston D35754; Yan Yean D35760; Warragul D35761; Portland D35762; Upper Beaconsfield D35764; Mt. Lovich D35766; Kalorama D35767, D35774; Sorrento D35768; Mt. Blackwood D35770; Brooklyn D35771; South Warrandyte D35772; 1.6 km N. of Darby River D35776-7; East Warburton D35783; 8 km N. of Cape Otway D35785; Blairgowrie D35788; Mt. William D35790; 8 km E.S.E. of Omeo D35791; Noojee D37829; Dartmouth Dam inundation area D39064-5, D41245, D41339, D41486, D41760, D41784, D41888, D41922, D42366; Falls Creek D35911; 16 km N.N.E. of Mt. St. Leonard D39569; 3.2 km S. of Mallacoota Airport D39577; 1.6 km S. of Mallacoota Airport D39578; Cobungra D39579; Mt. Howitt D42043; Davies Plain Creek D47527; Mt. Murphy D47613, D47662; 5 km W. of Marlo D47909.

Bass Strait. Curtis Island Group. (NMV) Curtis Island D39570-4.

Furneaux Island Group. (AM) Flinders Island R10524-5; Babel Island R13757; Great Dog Island R13758; (NMV) Babel Island D11839; Cape Barren Island D14298-300; Flinders Island, no precise locality R11039-40, D14301-2, D11840, D18141, D35773, Robert-dale D11739, Killiecrankie Bay D12331, Between Whitemark & Emta D13846, Deep Bight Gully D13855, Long Point D16527, North Pat's River D33772, Palana D35719, Wallanippi D35743-4, The Dutchman D35765, Ronga Cove D35784; Preservation Island D35703; West Sister Island D13856.

Kent Island Group. (NMV) R11037; Deal Island, no precise locality D4293-4, D8099,

D35742, D35781-2, D42097, D50361, Garden Cove D35713; Erith Island D35720, D35729-30, D50361.

King Island Group. (NMV) King Island R11023-4.

Tasmania. (SAM) Barn Bluff R5441; Cradle Mountain R12093-4; (AM) no data R6650A-C, R12760; Ouse River 6618, 6620-1; Mt. Wellington R5477-8; North Tasmania R7122; Fern Tree Glen R9465; Collins Vale R12043; (NMV) no data R11031, D4893; Circular Head R11034-5; Port Esperance R11042; Port Arthur D8352; near Lake Pedder D10935; Picton D10954, D11224; St. Mary's D13661; 3.2 km N.W. of Salt Water River D35704, D35706, D35786; 4.8 km N. of Todd Corner D35705; 2.4 km S.E. of St. Mary's D35707; 19.2 km W. of Smithton D35774; 2.4 km E. of Dee D35787; 6.4 km N. of Roseberry D35789; Maydena D39476.

***Drysdalia mastersii* (Krefft, 1866)**

Master's Snake

Hoplocephalus mastersii Krefft, 1866: 370. Type locality—Flinder's Range, S.A. Krefft, 1869: 63.

Denisonia coronoides Boulenger, (part) 1896: 336-337.

Denisonia coronoides var. *mastersii* [sic] Kinghorn, (part) 1929: 175.

Denisonia coronoides mastersii Kinghorn, (part) 1956: 164.

Drysdalia mastersii Worrell, (part) 1961: 25.

Worrell (part) 1963: 123.

Cogger, (part) 1975: 383.

Types: Krefft's original description dated 26th June 1866 and issued on 5th September stated that Mr. George Masters had found seven specimens in the Flinder's Range and it is assumed that the description was based on these specimens. Thus there may have been seven syntypes. One syntype was located in the British Museum of Natural History in 1973. This specimen (BM (NH) No. 1946.1.17.42, old number 66.6.13.2) is clearly shown in the Accessions Book to have been purchased from Mr. G. Krefft as "one of the types of *Hoplocephalus mastersii*" from the Flinder's Range on the 13th of June 1866. All catalogue entries, jar labels etc. carry the same information and this specimen was listed as "One of the

types of *H. mastersii*" by Boulenger in 1896 (page 337).

The Australian Museum Collection includes seven specimens of *D. mastersii* which could have been available to Krefft in 1866. Six of these, AM Nos. 6622-27, are recorded in the Register as having been collected in "S. Australia—?" and all were originally identified on Krefft's jar labels as *Hoplocephalus mastersii*. The seventh specimen, AM No. 6619, is recorded in the Register as having been collected from the "Ouse R. Tasmania G. Masters", presumably in error as specimens AM Nos. 6618, 6620 and 6621 are *D. coronoides* specimens with the same data. No Australian Museum reptile specimens were registered before Krefft left the Museum and the original Register data were taken from Krefft's jar labels (H. Ehmann, pers. comm.). It is possible that additional specimens of *D. mastersii* arrived at the Museum after Krefft had prepared the original description as Masters despatched two consignments of specimens from the Adelaide, Port Augusta, Port Lincoln and Flinder's Range areas in November 1865 but only one had arrived at the Museum by 18th January 1866. (H. Ehmann, pers. comm.).

From the above it can be seen that the British Museum (Natural History) received one definite syntype BM(NH) No. 1946.1.17.42 in 1866 and the Australian Museum collection contains seven specimens all of which may have been available to Krefft. Thus the collections of the British Museum of Natural History and the Australian Museum include eight possible syntypes.

In order to stabilize Krefft's name *mastersii* the only extant specimen which is undoubtedly one of Krefft's syntypes and for which reliable data is available has been selected as the lectotype.

Lectotype: BM(NH) 1946.1.17.42 (old number 66.6.13.2), British Museum of Natural History, London.

Locality: Flinder's Range, South Australia, purchased from G. Krefft.

Catalogue Reference: Boulenger (1896) specimen B.a.

Description: Snout-vent length 231 mm. Tail length 54 mm. Total length 285 mm. Scales round midbody 15. Ventral scales 134 (Boulenger, 1896, 140). Subcaudal scales undivided, 39. Anal scale undivided. Upper labials 6, 3rd and 4th subocular. Lower labials 7. Rostal contacts 1st labials, nasals and internasals. Single preoculars contact 2nd and 3rd labials, nasals, prefrontals and supra-oculars. Frontal contacts prefrontals, supra-oculars and parietals. Post oculars paired, contact supra-oculars, parietals, upper anterior temporals and 4th and 5th labials. Temporals 2 + 2.

Colour: Dorsal surface light brown, ventral surfaces light yellow speckled with black, ventral and subcaudal scales grey at margins. Distinct light yellow band two scales wide runs across the nape. Distinct white stripe edged above by black runs from below nostril under eye to neck.

Condition: Well preserved.

Comments: This specimen has been chosen as lectotype as it is the only available specimen which is clearly indicated as one of Krefft's types and also it agrees closely with the original description. In addition the lectotype has reliable documentation as all jar labels and entries in old and new accessions books, museum registers and published catalogues agree.

Paralectotypes: All the possible paralectotypes located are in the Australian Museum, Sydney.

Six specimens were recently tentatively added to the Australian Museum's type collection. These were AM Nos. 6622-27 collected from South Australia. For these specimens, ventral scale counts in order of current registration numbers are: 140, 143, 144, 141, 142, 134. Subcaudal scale counts in order of current registration numbers are: 37, 34, 38, 36, 41, 39.

A seventh Australian Museum specimen, AM No. 6619 registered as having been collected from Ouse River Tasmania by George Masters (see above) may have been available to Krefft. This specimen has 140 ventral and 43 subcaudal scales.

The ventral scales of these seven specimens

range from 134-144 with a mean of 140.6 and the subcaudals range from 34-43 with a mean of 38.3.

Coloration is as for the lectotype.

All seven specimens are conspecific with the lectotype.

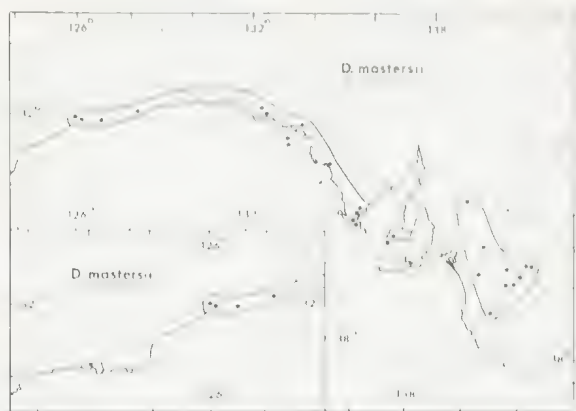


Figure 3—Map showing distribution of *Drysdalia mastersii*.

Other Specimens Examined

A further 60 specimens were examined.

Size: Largest adult: Snout-vent length 253 mm; tail length 62 mm; total length 315 mm. Juveniles at birth: Snout-vent length 83 mm; tail length 20 mm; total length 103 mm.

Scalation: Scales round midbody 15 in all specimens. Ventral scales range from 130-146 with a mean of 136.7 (N=58). Subcaudal scales were all undivided and ranged from 32-51 with a mean of 41.0 (N=57). Anal scale undivided in all specimens.

Colour: Juveniles at birth: Dorsal surface dark olive-brown ventral surface bright orange-red. Head darker than body, with a white stripe running along the upper lip from the nostril under the eye to the neck. Light yellow band across nape. Adults: Olive grey to olive green dorsal surface, ventral surface orange centrally, grey speckled with black laterally. Head darker than body, sometimes black, a white stripe edged

above with black running along the upper lip from the nostril, under the eye to the neck. A light yellow to off-white band two to three scale wide runs across the nape. Nape band normally narrowly broken on mid-line but often complete.

Localities and Registered Numbers:

No data. (SAM) R2334, R6648A-B.

Western Australia. (WAM) Eucla R18482, R24644; Cocklebidy R24668, R27470; 43 km S. of Madura R34417; 40 km S.S.E. of Mundrabilla R36717; Esperance R40009-10; 15 km S.S.E. of Cocklebidy R60811; South Australia (SAM) Ceduna R1165; West Coast R1600; Port Lincoln R2333, R2414, R11648, R11768, R11768A-B, R12903; Coombe R2362; Davenport Creek, West Coast R2455; Kulkami R4755; 3.2 km E. of Bleaford, Eyre Peninsula R4754A-C; "C" Island, Venus Bay R8996; Naracoorte R9305; End of Yorke Peninsula R9307; St. Francis Island R11775; Fennelon Island R12860; Nundroo, West Coast R14564; Koppio R14698; Scorpion Springs R15194; Stenhouse Bay R15327; (NMV) Fowlers Bay D4590-5; Kirton Point D8846-7; Port Lincoln D8855, D8945, D9042, D9086, D9209, D9537, D16496-500.

Victoria: (NMV) Yanac D11155; Telopea Downs D16502; Red Bluff D40197; 5.5 km W. of Wyperfeld National Park Office D51683; 18 km W. of Wyperfeld National Park Office D51718.

***Drysdalia rhodogaster* (Jan, 1863)**

Alecto rhodogaster Jan, 1863: 117. Type locality—Australia. Jan & Sordelli, 1873: 6, pl. 2, fig. 2.

Hoplocephalus collaris Macleay, 1887: 1111-2. Type locality—Bega, N.S.W. (As Goldman, Hill & Stanbury, 1969, do not mention this species, the type is presumed lost).

Denisonia coronoides Boulenger, (part) 1896: 336.

Pseudelaps minutus Fry, 1915: 93, fig. 7. Type locality—Colo Valley, N.S.W. = *Drysdalia mastersii* (Kretli, 1866) after Cogger 1979: 208.

Denisonia coronoides mastersii Kinghorn, (part) 1929: 175.

Denisonia coronoides mastersii Kinghorn, (part) 1956: 164.

Denisonia mastersii Worrell, 1956: 207, fig. 7 c-d.

Drysdalia mastersii Worrell, (part) 1961: 25. Worrell, (part) 1963: 123. Cogger, (part) 1975: 383.

Types: Jan (1863) described this species from a specimen (or specimens?) in the collection of the Hamburg Museum said to have come from Australia. Jan and Sordelli (1873) subsequently provided a clear illustration of a specimen, stating that it was in the Hamburg Museum and had come from Australia.

Unfortunately the Hamburg Museum catalogues and some of the type collections were destroyed by bombing during World War II (P. Grünwaldt pers. comm.). However, the general collection and many of the types survived intact with jar labels. Thus it is impossible to check directly from catalogues the number of specimens available to Jan or the status of any surviving specimen, and jar labels are the only primary source of information.

In 1863 Jan (p. 117) described five Australian species of *Alecto* from specimens in the Hamburg Museum. In 1973 a series of consecutively numbered specimens ascribed to these species on original jar labels were located in the Hamburg Museum collection.

These specimens, the corresponding Jan species names and their current identifications are as follows:

UHZ No. 476 *A. permixta* (= *Cryptophis nigrescens*)

UHZ No. 477 *A. rhodogaster* (= *Drysdalia rhodogaster*)

UHZ No. 478 *A. schmidtii* (= *Austrelaps superbus*)

UHZ No. 479 *A. dorsalis* (= *Unechis nigrostriatus*)

UHZ No. 480 *A. wiebeli* (= *Suta suta*)

Each of these species, with the exception of *A. wiebeli* were subsequently clearly illustrated by Jan and Sordelli (1873) from specimens in the Hamburg Museum. Comparisons of the specimens listed above with the relevant illustrations leave little doubt that they were the specimens figured. For these reasons it appears that the specimens listed above are the type specimens of Jan's respective species. In the case of *A. rhodogaster* we are satisfied that UHZ No. 477 is the holotype of Jan's species.

Holotype: UHZ No. R.00747 (old number 477). Universität Hamburg Zoologisches In-

stitut und Zoologisches Museum, Papendamm, Hamburg.

Locality: Australia (jar label and original description). No other data.

Description: Snout-vent length 248.5 mm. Tail length 65.6 mm. Total length 314.1 mm. Scales round midbody 15. Ventral scales 151. Subcaudal scales undivided, 51. Anal scale undivided. Upper labials 6, 3rd and 4th subocular. Lower labials 7. Rostral contacts 1st labials, nasals and internasals. Single preoculars contact 2nd and 3rd labials, nasals, prefrontals and supra-ocular. Frontal contacts prefrontals, supra-ocular and parietals. Post oculars paired, contact supra-oculars, parietals, upper anterior temporals and 4th and 5th upper labials. Temporals 2 + 2.

Colour: Dorsal surface greenish brown, ventral surface light grey, each ventral scale edged with dark grey. Snout and anterior portion of head similar to the body, but stippled with black, the stippling becoming denser posteriorly, until a darker colour predominates with a greenish-brown stippling from approximately a mid-line between the eyes. A pale orange coloured band across the nape, two to three scales in width. Sides of head greyish, with a series of longitudinal spots forming a dark stripe from immediately anterior to the nostril, through the eye, to the anterior edge of the nape band.

Condition: Well preserved.

Hoplocephalus collaris Macleay 1887, was described very adequately and the description agrees with *D. rhodogaster* as recognized here. In addition, the type locality (Bega, N.S.W.) is well within the known range of *D. rhodogaster*. The type specimen has not been located, and, as it was not mentioned in Goldman, Hill and Stanbury (1969) or Cogger (1979), is presumed lost.

Pseudelaps minutus Fry 1915, described from specimens from N.S.W. was placed in the synonymy of *D. mastersii* by Cogger (1979). The holotype, collected from Colo Valley,

N.S.W. (Reg. No. AM R3971) is conspecific with the holotype of *D. rhodogaster* and is transferred to the synonymy of that species here. The paratypes (Reg. Nos. AM R6643 and R6646) are also conspecific with the holotype of *D. rhodogaster*.

Other Specimens Examined

A further 35 specimens were examined, all from eastern New South Wales from the Blue Mountains in the north, to the Pambula area in the south.

Size: Largest adult: Snout-vent length 362 mm; tail length 98 mm; total length 460 mm. Juveniles at birth: Snout-vent length 111 mm; tail 28 mm; total length 139 mm.

Scalation: Scales round midbody 15. Ventral scales ranged from 141-155 with a mean of 147.2 (N=33). Subcaudal scales were all undivided and ranged from 41-54 with a mean of 47.8 (N=31). Anal Scale undivided in all specimens.

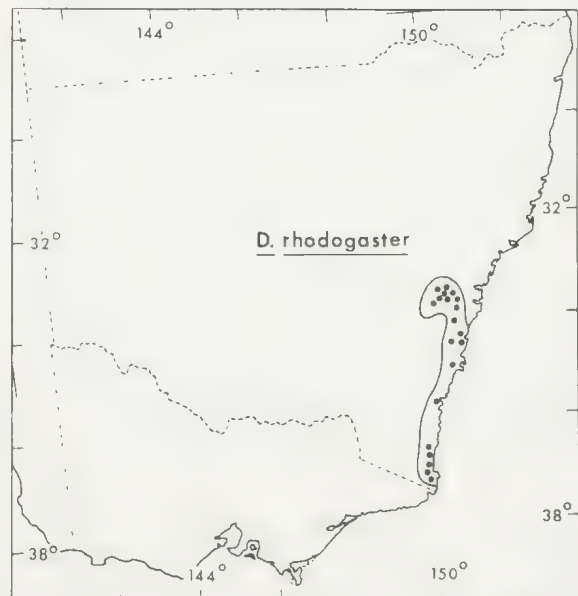


Figure 4—Map showing distribution of *Drysdalia rhodogaster*.

Colour: Juveniles at birth: Dorsal surface very dark brown, ventral surface orange-red. Head darker than body, snout dark brown, top of head black. Upper lip dark brown with a black stripe from nostril to eye and a broken black stripe from below eye to neck. Distinct light orange band across nape. Adults: Dorsal surface brown to olive-green, ventral surface yellow to orange. Snout same colour as body speckled with black, top of head black. Black stripe from nostril to eye and a broken black stripe from below eye to neck. A distinct light orange to light brown band 2 to 3 scales wide runs across nape, sometimes reduced to an ill defined lighter coloured patch.

Localities and Registered Numbers: New South Wales. (AM) Pambula R2386, R2433; Hazelbrook R6139; Barrangarry R7748, R7961, R10542-3; Macquarie Pass R11088; Jenolan Caves R11364; Lawson R11888; Wongawilli, via Dapto R12556; Leura R15074; Hurstville (?) R15085; Woodford R15299; Lockin Hill, near Shellharbour R17172; Batemans Bay R20751; Wentworth Falls R21046; Robertson R28260; Bilpin R29738; Merimbula R37373; Faulconbridge R40803; Bega R42062; Catherine Hill, near Picton R47279; Conjola R47404; (NMV) Katoomba D14314; Blackheath-Mt. Victoria D14315-8; Lawson D14319; Medlow Bath D16501; Ben Boyd National Park D47969; Blackheath D50482-3; Blue Mountains D50484; 5 km W. of Kiah D50563.

Ecology

Habitat: *D. coronata* and *D. coronoides* occur mainly in tussock grasslands, grassy woodlands and associated swampy areas. *D. coronoides* also occurs in subalpine and alpine habitats. *D. mastersii* and *D. rhodogaster* on the other hand occur mainly in drier habitats and appear to be restricted to heathlands.

Food: The diets of the four species are discussed in detail by Shine (In press). The major food of *D. coronoides*, *D. mastersii* and *D. rhodogaster* are heliothermic skinks which comprise about 90% of food items. *D. coronata* has two major food sources as skinks and

frogs each comprise roughly 50% of all food items.

Thermoregulation: All species are shuttling heliotherms (*sensu* Rawlinson, 1974) basking only when necessary to elevate body temperature above the voluntary minimum and spending the rest of the activity period foraging in the shade. This assessment is confirmed by the analysis of prey items where heliothermic skinks predominate. *D. coronoides* (and possibly the other species) will also actively forage for food on warm evenings.

Thermal preferences are only available for *D. coronoides* and this species has a voluntary minimum body temperature of 24.8°C, a mean preference of 31.1°C and a voluntary maximum of 37.7°C (Rawlinson, 1974).

Reproduction

The reproduction of all species is discussed in detail by Shine (In Press). All species are viviparous and clutch sizes range from 2-10 with means ranging from 2.8 (*D. mastersii*) to 5.4 (Tasmanian *D. coronoides*). The young are born from late February to mid April (Rawlinson, 1974; Shine In Press).

Relationships

All four species are closely related and considered to be monophyletic with the species falling into two natural groups. The first group comprises *D. coronata* and *D. coronoides* which have differentiated across southern Australia. The second group comprises *D. mastersii* and *D. rhodogaster* which have differentiated in south-eastern Australia. Within the groups the relationship between *D. coronata* and *D. coronoides* does not appear to be as close as the relationship between *D. mastersii* and *D. rhodogaster*.

McDowell (1967) discussed the head musculature and hemipenial structure of many elapid snakes including *D. coronata* and *D. coronoides*. He concluded that these two species showed a relationship to the elapid genera *Notechis*, *Tropidechis* and *Oxyuranus*. Further, he stated that *D. coronata* appears to be a genuine evolutionary intermediate between *D.*

coronoides and *Notechis* as he could find no internal feature to separate *D. coronata* from *Notechis* despite the close resemblance between external features of *D. coronata* and *D. coronoides*. McDowell suggested that *D. coronata* may merit generic distinction.

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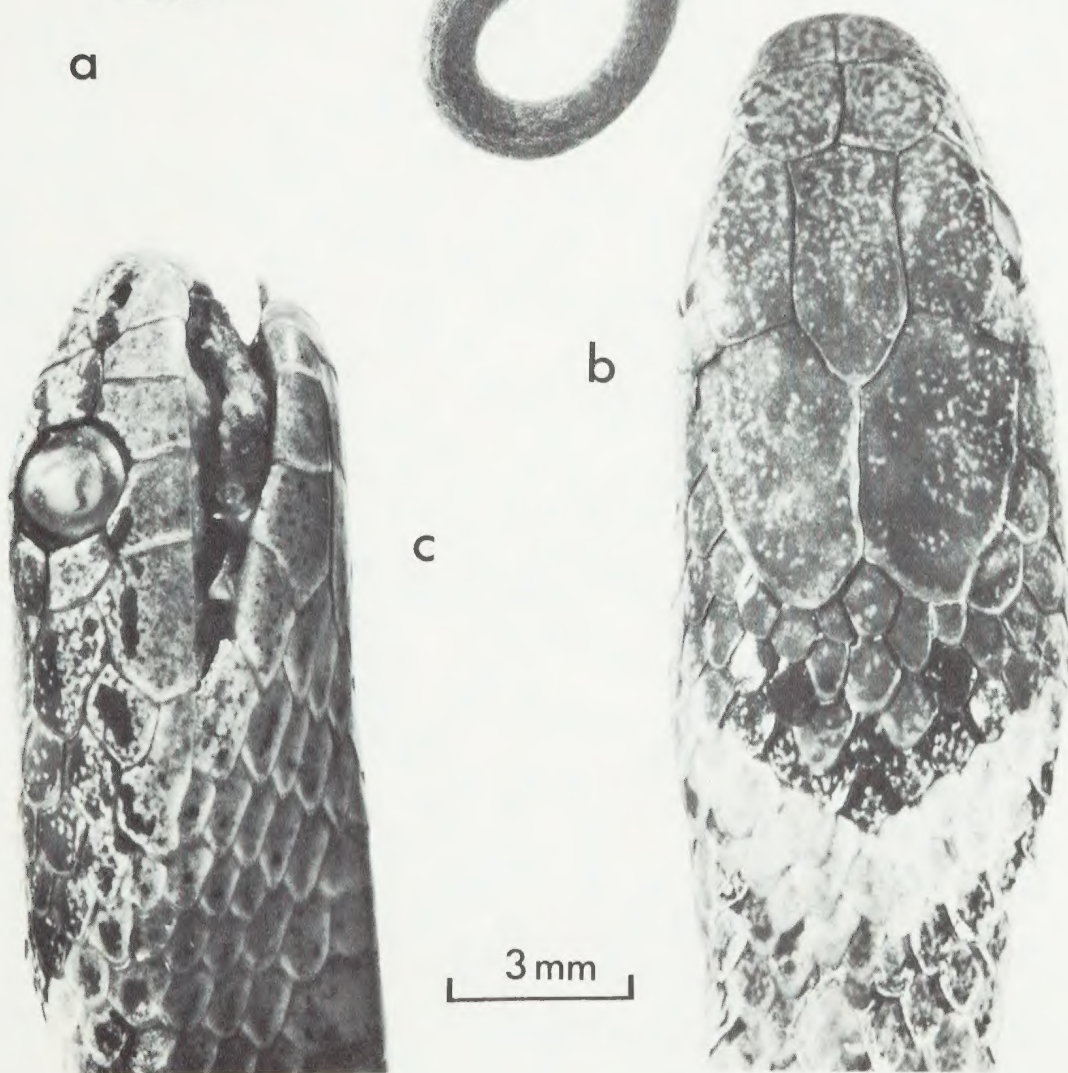
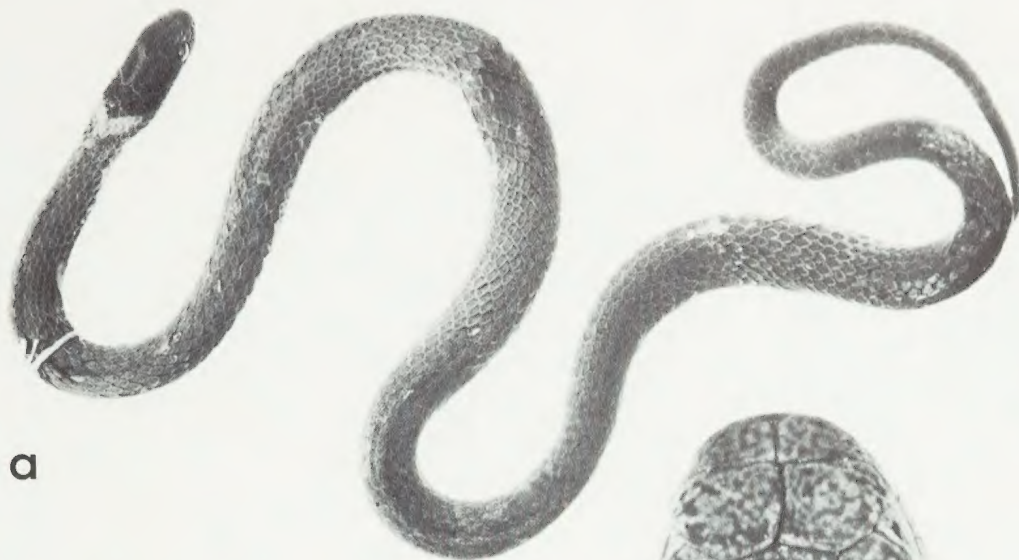
TABLE 1
Ratio of length of frontal scale by width.

Species	Max.	Min.	Mean	N
<i>D. coronata</i>	2.11	1.56	1.78	30
<i>D. coronoides</i>	2.66	1.90	2.24	44
<i>D. mastersii</i>	2.81	2.00	2.41	21
<i>D. rhodogaster</i>	3.16	2.00	2.39	7

Explanation of Plate

PLATE 12

- a. Dorsal view of Holotype of *Drysdalia rhodogaster* (Jan), total length 314.1 mm.
- b. Dorsal view of head of Holotype of *Drysdalia rhodogaster* (Jan).
- c. Lateral view of head of Holotype of *Drysdalia rhodogaster* (Jan).



3 mm

